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Reproductive Strategies in a Tropical Anuran Community

By
Martha L. Crump

UNIVERSITY OF KANSAS
LAWRENCE 1974

November 15, 1974

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November 15, 1974

Reproductive Strategies in a Tropical Anuran Community

By

Martha L. Crump

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The University of Kansas, 1974.

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INTRODUCTION

If it is not small enough to eat nor large enough to eat you, and does not put up a squawk about it, mate with it. D. L. Jameson (1955).

But, reproduction in frogs is more complicated than Jameson's whimsical statement indicates. Six years ago, when I collected my first tropical frogs, I was immediately impressed with the diversity of the fauna. My first surprise was finding more than 35 sympatric species of frogs within the first week. I encountered the flashy and gaudy color patterns, such as those of the *Hyla leucophyllata* group, and the morphological oddities, such as *Hemiphractus* and *Pipa*. However, the most impressive aspects of the diversity were the bizarre modes of reproduction. Being a temperate-zone biologist, I was accustomed to the "generalized" life history of frogs—egg deposition in water, aquatic larval development, metamorphosis, following which the frogs spend most of their lives on land. But many tropical species lay their eggs out of water and have aquatic larvae, and others have completely eliminated the tadpole stage. It seems as though evolutionary forces operant on tropical frogs favored more "imaginative" life histories than those of temperate frogs.

The greatest anuran species richness of any area in the world studied to date is found at Santa Cecilia, Ecuador (81 species). Upon examination of the modes of reproduction (egg deposition site and type of development), it is apparent that a great diversity of modes exists—probably the greatest in any known region. It seems reasonable to assume that as anuran speciation occurred in the tropics, the evolutionary thrust included this diversity of reproductive modes. Environments, as measured by niche diversification, life span of the habitat, and climatic variables, as well as competition and predation no doubt operated on the genetic potential of organisms in bringing about physiological, morphological, and behavioral changes. These influenced and were influenced by the evolution of reproductive diversity.

The premise of this study is that the reproductive diversity at Santa Cecilia allows coexistence of a great number of anuran species by means of partitioning of breeding sites. In order to investigate this premise, I have analyzed the reproductive strategies operant within a diverse community of Neotropical frogs. Several aspects of the reproductive characteristics of each species of frog are considered: (1) behavioral and morphological adaptations, (2) habitat partitioning as judged by egg deposition site, (3) temporal partitioning of the environment judged by breeding seasonality, (4) size-fecundity relationships, (5) volumetric relationships of female to egg-complement volume, and (6) developmental relationships (number of eggs deposited, size of eggs, number of days until hatching, size at hatching), as related to the egg deposition and developmental sites. The data are synthesized into a discussion incorporating interpretation of reproductive strategies in terms of spatial and temporal environmental partitioning, reproductive effort of the adult frogs, and the ecological and evolutionary significance of the reproductive diversity.

Acknowledgements

I am extremely grateful to the many persons who assisted in the conception, gestation, and finally in the deliverance of this study. Dr. William E. Duellman first aroused my curiosity concerning anuran reproductive strategies years ago and later served as chairman of my doctoral committee. For all of this, and especially for instilling within me a love for the tropics, I am indebted.

Special thanks go to John E. Simmons, my loyal and handsome field assistant, who provided much assistance as well as comic relief; he made it his duty to keep me humble and provided much encouragement and moral support. In John's absence, Benancio guided me in the forest. Numerous other persons helped with field work: Joseph T. Collins, William E. Duellman, Mario Durán, Abraham Goldgewicht, Philip S. Humphrey, Steve Humphrey, and Linda Trueb. I thank my hosts Ing. and Sra. Ildefonso Muñoz B. for their warm hospitality at Santa Cecilia, and especially for keeping my plate filled with rice. Plane transportation between Quito and Lago Agrio was provided by Texaco and Gulf Petroleum companies.

Enlightening and thought-provoking discussions with numerous persons have improved the quality of this study. Among those from whom I have benefited are William E. Duellman, Philip S. Humphrey, Julian C. Lee, Norman A. Slade, Orley R. Taylor, Catherine A. Toft, Linda Trueb, and Richard J. Wassersug. To each I am grateful for suggestions and comments regarding the written and re-written manuscript. I thank Sally Cool for typing the tables and Linda Trueb for offering critical, editorial suggestions.

I am ultimately grateful to the various foundations and organizations which provided financial support. Field work during 1971-72 was supported mainly by the National Science Foundation (GB-29557) and the Organization for Tropical Studies; additional support was provided from a National Science Foundation grant (GB-8785, Robert S. Hoffmann, principal investigator). Monies from the William Saul Fund, the Graduate School, and the College Foreign Study Committee, all from the University of Kansas, enabled the completion of field work in 1973. Preparation of the manuscript was done while supported by a National Science Foundation grant (GB-35483, William E. Duellman, principal investigator).

Description of Study Site

Santa Cecilia is a small Quecchua Indian village located on the north bank of the Río Aguarico, a tributary of the Río Napo, in the upper Amazon Basin in eastern Ecuador (Fig. 1). The village is situated at 00°06′ N, 76°51′ W, at an elevation of 340 meters. Maximum relief in the area is less than 20 meters. The soils along the Río Aguarico are sandy, and the forest soils are mostly laterites with a layer of humus and leaf litter several centimeters in depth. Rainfall is aseasonal, although there are wetter and drier months. My weather records indicate that for the period July 1971-June 1972, the driest months were August (220.5 mm), September (251.5 mm), and February (243.0 mm); the wettest were October (422.0 mm), November (530.5 mm), and March (619.0 mm) (Fig. 2). Total annual rainfall accumulation was 4279.0 mm. Local residents claimed that the wet and dry patterns of that particular year were typical. The maximum temperature in the shade during the year was 35°C, and the minimum temperature at night was 18°C.

Biological field studies at Santa Cecilia were initiated by The University of Kansas in November 1966. Between then and June 1971, about 23 man-months of field work were spent surveying the herpetofauna and recording basic ecological observations. When studies began at Santa Cecilia, the area was mostly covered with primary rain forest, consisting of both swamp and high-ground forests. However, by 1971 much of the area had been cleared by settlers so that most of the immediate area (3 km^2) is now partially lumbered or under agriculture.

Methods

Field work at Santa Cecilia was carried out from June 1971 through mid-July 1972 and April-May 1973. The initial 13 months was divided into 20 periods of time, each of 20 days (except for the last period, of 15 days). Calling activities of males and reproductive con-

Fig. 1.—Map of Ecuador showing the location of Santa Cecilia.

ditions of females were recorded for as many species as possible within each 20-day period. Species assemblages (composition, abundance, and activity) at certain ponds were recorded at regular intervals throughout the year to obtain information on spatial and temporal utilization of breeding sites. Collections and observations were made both by day and night. The present study deals with 74 of the 81 species known from Santa Cecilia. The other seven species were not obtained during 1971-72; volumetric data were accumulated during April-May 1973. Size-fecundity data were recorded mainly from individuals collected during 1971-72. For those species represented by less than 20 gravid females, mature ovarian eggs were counted from individuals collected from Santa Cecilia in previous years whenever possible. Daily weather data consist of maximum

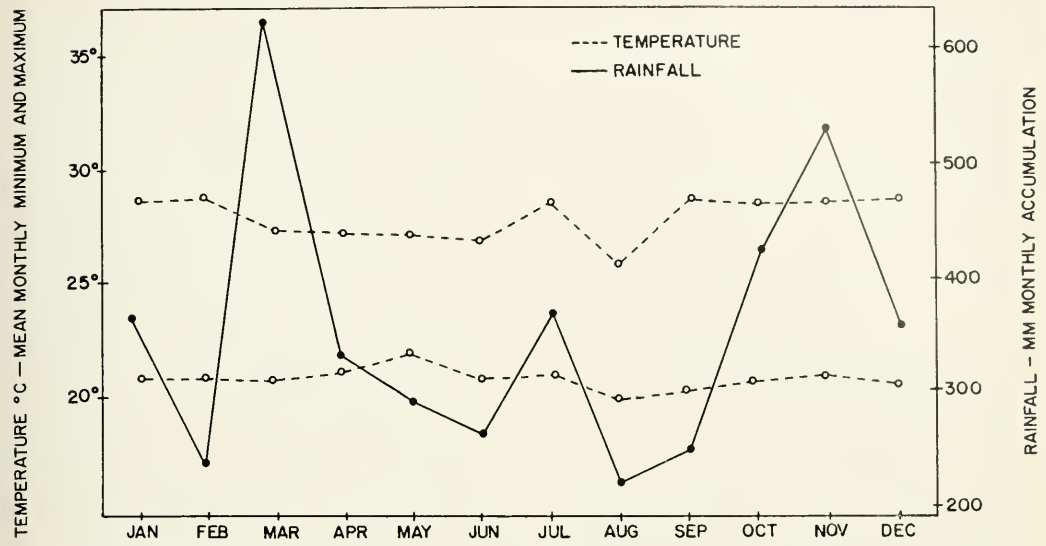

FIG. 2.—Monthly mean minimum and maximum ambient air temperatures and monthly rainfall accumulation for the period July 1971-June 1972.

and minimum ambient temperature (in thatched shelter), rainfall accumulation, and phase of the moon and associated cloud cover.

Field work was carried out in a 3 km^2 area. Three main forest trails were worked in addition to a variety of clearings and other disturbed, forest-edge environments (Fig. 3). Primary forest about 3 km west of Santa Cecilia also was studied; several species of frogs were found either exclusively or in greater abundance there. This area consists of both swampy depressions and high-ground, mature forest. The canopy is about 85 percent closed; the ground cover is more sparse and the leaf litter deeper than in the forest immediately around Santa Cecilia.

Eight aquatic sites were investigated extensively throughout the year (Fig. 3). *Ephemeral* refers to those aquatic environments with a life span of generally less than two weeks. *Temporary* sites are those in which water is present for at least two weeks at a time, but are known to dry up. The *permanent* environments were filled with water throughout the study period. The sites are as follows: (1) Air Strip Edge Ditches (5-20 $\times$ $<$ 1 m). The Texaco Petroleum Company cleared an air strip at Santa Cecilia in late 1964; continued maintenance results in much forest-edge habitat. The ditches along the edge of the air strip are often filled with water and are considered ephemeral environments; (2) Clearing Swamp—water-filled depression (12 $\times$ 5 m) amidst dense, grassy vegetation in a man-made clearing; (3) Forest Edge Swamp A—temporary swamp (15 $\times$ 7 m) by the edge of a road, surrounded on three sides by second-growth forest; (4) Forest Edge Swamp B—temporary swamp (8 $\times$ 5 m) by the edge of a road, immediately surrounded by dense, grassy vegetation and second-growth forest; (5) Heliconia Swamp—relatively large (50 $\times$ 15 m), temporary forest swamp choked with broad-leafed *Heliconia* plants; (6) Second-growth Forest Swamp—permanent, forest swamp (70 $\times$ 15 m) in thick vegetation; (7) Palm Pond—large, permanent pond (100 $\times$ 30 m) in mature forest, with the depression filled with spiny palm trees; and (8) Lake—permanent, deep lake (300 $\times$ 100 m) in second-growth forest. In addition, numerous temporary swamps and the river edge were studied.

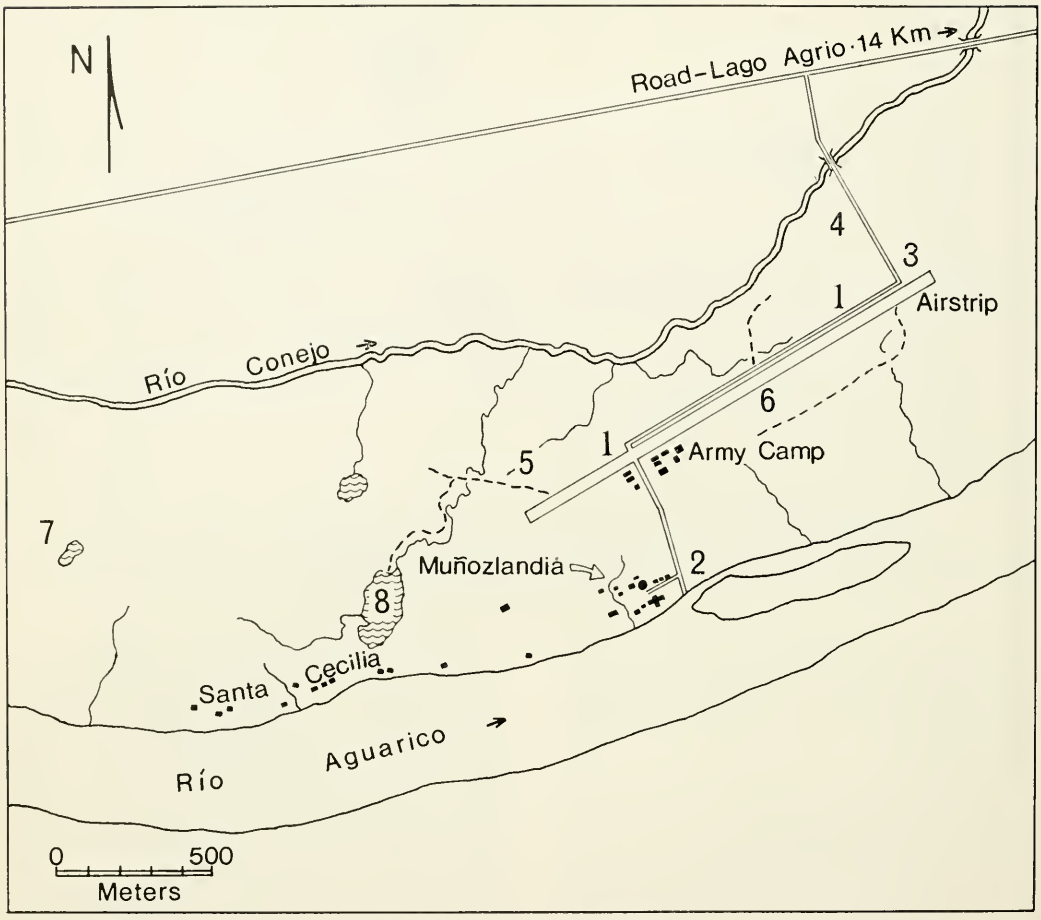

Fig. 3.—Map of Santa Cecilia showing the three main forest trails (indicated by dashed lines) and the eight aquatic breeding sites: (1) Air Strip Edge Ditches, ASED; (2) Clearing Swamp, CS; (3) Forest Edge Swamp A, FESA; (4) Forest Edge Swamp B, FESB; (5) Heliconia Swamp, HS; (6) Second-Growth Forest Swamp, SGFS; (7) Palm Pond, PP; and (8) Lake, L.

In order to determine size-fecundity relationships, series of individuals of each species for which gravid females were found in sufficient abundance were preserved throughout the study period. Fecundity measures are based on ovarian complement (number of "mature" ovarian eggs). I am unable to define "mature eggs" because the criteria are species-specific. The larger the eggs, the better developed they are; thus, an arbitrary cut-off point for each species was used. In those species with non-pigmented eggs, generally the more yellow (as contrasted to white) the eggs, the more mature they are. Pigmented eggs generally become darker with maturity. Snout-vent length and egg diameter were measured with a millimeter rule and recorded to the nearest 0.5 mm. Volumetric relationships were based on ovarian complement rather than ovulated eggs because the latter less frequently are encountered for the majority of the species studied. Frog and egg volumes were determined by means of water displacement; measurements were taken to the nearest 0.1 or 1.0 ml in graduated cylinders. A gallon jar containing 250 ml of water, calibrated to the nearest 10 ml, was used for the two large species. Developmental data for species with aquatic

larvae were obtained by placing either amplectant pairs or males and gravid females together in plastic containers with water and vegetation. Amplectant pairs of *Eleutherodactylus* were placed in containers with soil, bark, and leaves. Once eggs were deposited, adults were removed, and the eggs counted ("clutch size"), and diameters of 10 eggs measured. Containers with developing eggs were kept in one area of the laboratory (a thatched shelter), away from direct sunlight. The developing embryos were checked several times daily, and hatching times recorded when approximately 50 percent of the tadpoles had broken through the egg membrane. Generally, the time span between the first and last hatching was less than ten hours.

Variables were checked for normality (g_1 and g_2 statistics) and homogeneity of variances (F_{max} test) in all statistical analyses involving parametric tests (Sokal and Rohlf, 1969); results are included in the appropriate tables. In certain cases, data were transformed to their natural logs to eliminate curvilinearity and minimize the spread of data points. In other instances, log transformation was used to produce normal distribution of data points. The community matrix is based on species associations obtained from similarity coefficients, using the equation $S = n_{jk}/n_{jk} + u$), in which u = number of characters in unmatched cells, and n_{jk} = number of paired positive characters (Sokal and Sneath, 1963). Ovarian size factor (Duellman and Crump, 1974) is an index of egg mass relative to body length (CS(OD)/SVL, in which CS = mean clutch size, OD = mean ovum diameter, and SVL = mean snout-vent length of the gravid females).

Specimens have been deposited in the herpetological collection at the Museum of Natural History, The University of Kansas.

SPECIES COMPOSITION AND MODES OF REPRODUCTION

Eight families of frogs are represented at Santa Cecilia: Pipidae (1 species), Leptodactylidae (25 species), Bufonidae (4 species), Dendrobatidae (5 species), Hylidae (37 species), Centrolenidae (3 species), Microhylidae (5 species), and Ranidae (1 species), a total of 81 sympatric species. Several of the species seem to be endemic to the upper Amazon region. The distribution of others is peripheral to the Amazon Basin or on the eastern slopes of the Andes, whereas others are widespread in the Amazon Basin.

Concerning the distribution of frogs in the New World, of the eight families of frogs at Santa Cecilia, none is exclusively South American. Three are found only in Central and South America (Centrolenidae, Dendrobatidae, and Pipidae), and the other five families are found in North America as well as in Central and South America. Of the 25 genera at Santa Cecilia, ten are endemic to South America (*Ceratophrys, Ctenophryne, Dendrophryniscus, Edalorhina, Hamptophryne, Ischnocnema, Lithodytes, Nyctimantis, Osteocephalus,* and *Sphaenorhynchus*). The remaining 15 genera are found in Central America; the origin and distribution of these genera have been discussed by Savage (1966). He referred to the genus *Rana* as being "extratropical North America." Only one species occurs in South America. Five genera are considered "widespread tropical" (equally strong species differentiation in Central and South America): *Bufo, Eleutherodactylus, Hyla, Phrynohyas,* and *Phyllomedusa.* The remaining nine genera are considered "South American" (centers of distribution and differentiation in South America).

As used here, mode of reproduction is a combination of oviposition site and type of development. I recognize 10 modes within the frog fauna at Santa Cecilia: (1) eggs deposited in ditches, puddles, swamps, ponds, lakes, and streams, with free-swimming aquatic larvae; (2) eggs deposited in tree cavity above ground, with free-swimming aquatic larvae; (3) eggs deposited in basin constructed on ground by the male,

with free-swimming aquatic larvae; (4) eggs deposited on vegetation above water, with free-swimming aquatic larvae (tadpoles hatch and fall into water); (5) eggs deposited in foam nest on or near water, with free-swimming aquatic larvae; (6) eggs deposited on land, with free-swimming aquatic larvae (tadpoles carried to water on dorsum of adult); (7) eggs deposited in foam nest on land and larvae develop within foam; (8) eggs deposited out of water, with direct development; (9) eggs carried in depressions on dorsum of aquatic female, with direct development; (10) eggs carried in depressions on dorsum of terrestrial female, with direct development. See Appendix 1 for a complete list of the species found at Santa Cecilia and their corresponding reproductive mode. These modes of reproduction may be classified generally into three groups on the basis of oviposition site and development of the young in relation to water (Table 1).

A total of 36 species from five families deposit eggs in open, unprotected bodies of water, in which subsequent larval development occurs. The range in snout-vent length of these species is 19.0 mm to 132.0 mm. Some are terrestrial, others arboreal; some breed in forest or forest-edge environments, others in open, disturbed areas. Most of these species lay many eggs.

Table 1.—Modes of Reproduction of the Anuran Fauna at Santa Cecilia.
The numbers in parentheses indicate the seven species not found during the present study.

Site of Development	Pipidae (1 species)	Leptodactylidae (25 species)	Bufonidae (4 species)	Dendrobatidae (5 species)	Hylidae (37 species)	Centrolenidae (3 species)	Microhylidae (5 species)	Ranidae (1 species)	Total
I. Eggs + larvae in water									
A. Mode 1—unconstrained body of water	-----	(1)	4	-----	21	-----	4	1	
B. Mode 2—tree cavity above ground	-----	-----	-----	-----	(2) 1	-----	(1) -----	-----	36 species
C. Mode 3—constructed basin	-----	-----	-----	-----	1	-----	-----	-----	
II. Eggs out of water; larvae develop in water									
A. Mode 4—eggs on vegetation above water	-----	-----	-----	-----	11	2	-----	-----	25
B. Mode 5—eggs in foam nest; tads in water	-----	5	-----	-----	-----	(1) -----	-----	-----	species
C. Mode 6—eggs on land; larvae carried to water	-----	(1) -----	-----	5	-----	-----	-----	-----	
III. Neither eggs nor larvae unprotected in water									
A. Mode 7—eggs and tads in terrestrial nest	-----	1	-----	-----	-----	-----	-----	-----	
B. Mode 8—non-aquatic eggs; direct development	-----	14	-----	-----	-----	-----	-----	-----	17
C. Mode 9—eggs and young buried in pits of dorsum-aquatic	(1)	-----	-----	-----	-----	-----	-----	-----	species
D. Mode 10—eggs and young attached to dorsum-terrestrial	-----	-----	-----	-----	1	-----	-----	-----	
IV. Mode of reproduction unknown	-----	3	-----	-----	-----	-----	-----	-----	3 species

A survey of the order Anura indicates an evolutionary trend in reproduction toward terrestriality (Goin, 1960). As in most animals, the immature stages of amphibians are particularly vulnerable to predators. The anuran fauna at Santa Cecilia illustrates many of the ways in which problems associated with egg deposition and larval development in open water have been alleviated. The larvae of some species in mode 1 have accelerated development; their "strategy" is to metamorphose and leave the water as soon as possible. The two species representing modes 2 and 3 deposit eggs in isolated sites, thereby reducing vulnerability of the eggs and aquatic larvae to certain environmental hazards and predators.

Another group (25 species) deposits eggs out of water, but retains larval development. Four families exhibit convergence toward this evolutionary step reducing vulnerability of eggs (modes 4-6). Centrolenids and hylids deposit eggs over standing or running water; upon hatching, the tadpoles drop into the water and undergo further development. Dendrobatids deposit large terrestrial eggs; subsequently, the tadpoles are carried to water on the dorsum of an adult. Many leptodactylids produce foam nests in which eggs are suspended. The nests are placed either on the water surface or near water, and the hatchlings undergo aquatic development. In addition to the adult behavioral and physiological modifications from the generalized reproductive mode, some species exhibit morphological adaptations associated with these modes of reproduction. Likewise, the larvae exhibit morphological adaptations for the "unconventional" entrance into the aquatic environment. These morphological modifications are discussed later.

A third group (17 species) shows convergence in the evolutionary step of total independence from water, in that neither eggs nor young are left unprotected in water (modes 7-10). One leptodactylid produces a foam nest with egg suspension on land, and the larvae undergo complete development and metamorphosis within the nest. Fourteen other leptodactylids deposit nonaquatic eggs. The free-swimming, aquatic larval stage is completely eliminated and the young hatch directly into small froglets. Two species, one aquatic and one terrestrial, exhibit complete parental care. The eggs of both species are either buried or attached to the dorsum of the female; development is direct in both species.

The mode of reproduction is unknown for three leptodactylids. Predictions concerning these species appear in the synthesis of results section; the suggestions are predicated on ovarian egg complement size.

BEHAVIORAL AND MORPHOLOGICAL REPRODUCTIVE ADAPTATIONS

Numerous surveys have concerned evolutionary trends in amphibian reproductive modes and descriptions of life histories (Goin, 1960; Harvey, 1963; Jameson, 1955, 1957; Lutz, 1947, 1948; Lynn, 1961; Noble, 1927, 1931; Orton, 1951; Tihen, 1965). A commonly proposed evolutionary trend in reproduction is that frogs have evolved toward greater terrestriality. The "generalized" frog is considered to have mode 1 reproduction, in which eggs are deposited directly in water and development occurs therein. About 46 per cent of the species of frogs at Santa Cecilia exhibit this mode of reproduction. The remainder have specialized oviposition sites and/or direct development. And, many species possess specialized behavioral and/or morphological modifications.

Male *Hyla boans* construct basins in sand, gravel, or mud along the edge of the river. Adult males have a protruding prepollex (vestigial digit on the inner side of the first digit on the forefoot) and a long, curved prepollical spine. The spine probably aids in grasping the female during amplexus. Lutz (1960) ob-

served aggressive behavior between male *Hyla faber* [same species group as *H. boans* and *H. rosenbergi;* same mode of reproduction (Duellman, 1970)], and claimed that the spines were used in physical combat. The eggs are heavily pigmented; they are deposited as a surface film, probably to maximize respiration area in the oxygen-poor environment typical of shallow, small bodies of water. Duellman (1970) described tadpoles of this species from Panamá as follows: "Hatchling tadpoles have a total length of about 4.5 mm. Large, filamentous gills and prominent oral suckers are present; the yolk sac is still large." Noble (1931) described the tadpoles of the closely related species, *Hyla rosenbergi,* as having "enormous pinnate gills which adhere to the surface film of the basin." The feather-shaped gills are probably an adaptation to the low supply of oxygen in the basins.

There are four groups of anurans that deposit eggs on vegetation above water: (1) centrolenids (2 species), (2) phyllomedusines (4 species), (3) *Hyla leucophyllata* group (5 species), and (4) *Hyla parviceps* group (2 species). The phyllomedusines possess opposable thumbs. The female searches for a suitable oviposition site above water, with the male on her dorsum during amplexus; because most phyllomedusines are heavy-bodied, the opposable thumb likely evolved as an adaptation for increased arboreal efficiency. Male *Phyllomedusa* have horny nuptial excrescences on the thumbs; presumably these aid in grasping the female during amplexus. The other hylids of this mode and the centrolenids lack these structures. The centrolenids and phyllomedusines deposit non-pigmented eggs, whereas the species of *Hyla* deposit lightly to heavily pigmented eggs. *Centrolenella munozorum* deposits eggs on the underside of leaves; the oviposition site is unknown for *Centrolenella midas.* The *Hyla* deposit eggs on the upper surfaces of leaves. Usually *H. bokermanni* and *H. brevifrons* deposit eggs on the distal tips of leaves, whereas members of the *Hyla leucophyllata* group often deposit eggs on the middle of the leaf. *Phyllomedusa palliata* deposits its clutch on the upper surface of leaves, usually at the distal tip nearest the water. *Phyllomedusa tarsius,* in contrast, encloses the egg mass with leaves ("closed nest"). This reduces the exposed surface of the clutch and presumably lowers desiccation rates and reduces loss due to predation. Five egg clutches of *P. tarsius* were observed at Santa Cecilia. The clutch consists of both empty gelatinous egg-capsules and egg-containing capsules (Fig. 4). All had eggs dispersed throughout the entire clutch, although the top and bottom of the egg mass generally consisted of mainly eggless capsules. Agar (1909) described this characteristic of the closed nest of *Phyllomedusa sauvagii* in detail. He suggested that the empty egg-capsules have a three-fold function: the plugs at the top and bottom of the nest provide protection from the sun and air, the empty capsules provide an extra source of fluid for the developing embryos, and the plug at the bottom serves to keep the entire nest intact until hatching occurs.

The eggs of six species of Leptodactylidae are suspended in a frothy mass of mucus, air, and water ("foam nest"), produced by kicking of the male during amplexus. Adult male *Leptodactylus pentadactylus* and *L. wagneri* have prepollical spines; these seem to facilitate amplexus, because mated pairs of these species are quite active. In addition, the former species has a cluster of horny spines on the chest and greatly enlarged forearm muscles. Heyer (1969) discussed the adaptive shift between the aquatic and terrestrial zones as demonstrated by species of *Leptodactylus.* He divided the species into five groups based on oviposition site. The groups, with the corresponding representatives from Santa Cecilia, are as follows: (1) *L. melanonotus* group—*L. discodactylus* and *L. wagneri;* (2) *L. ocellatus* group—no species at Santa Cecilia; (3) *L. pen-*

FIG. 4.—*Phyllomedusa tarsius* egg clutch, showing empty gelatinous egg-capsules. Mean egg diameter is 3.5 mm.

tadactylus group—*L. pentadactylus;* (4) *L. fuscus* group—*L. mystaceus;* and (5) *L. marmoratus* group—*L. andreae.* L. *discodactylus* and *wagneri* reflect the primitive *Leptodactylus* pattern in that the foam nest is placed on top of the water (Heyer, 1969). *L. pentadactylus* shows the first step towards terrestriality; nests are placed in cavities or potholes by the edge of water, thus providing protection from pond predators. The next adaptive step is that represented by *L. mystaceus,* in which the nest is placed in a burrow made by the male. Partial larval development occurs within the nest, thereby giving the tadpoles a potential developmental advantage (i.e. earlier metamorphosis) over the other species of larvae in the aquatic environment. Heyer also suggested that possibly the species of the *L. fuscus* group avoid much food and space competition in the pond. The egg masses of these species are less subject to desiccation than the more exposed nests of groups 1-3. *L. andreae* represents the most specialized type of reproductive behavior and larval development; this species is completely independent of standing bodies of water. The nest is produced in an "incubating chamber" similar to that made by members of the *L. fuscus* group. All larval development occurs within the nest; the young feed entirely upon the large yolk stores from the eggs.

There is a trend towards decrease in numbers of eggs per nest and increase in egg diameter from the most aquatic (groups 1-2) to the most terrestrial (group 5) groups. In general, those species depositing eggs in more exposed situations (*L. pentadactylus* and *wagneri*) have pigmented eggs, whereas those using more sheltered situations (*L. andreae* and *mystaceus*) lack melanophores. An exception is *L. discodactylus,* which, although it places the nest on the water surface, has non-pigmented

eggs. Zweifel (1968) discussed two adaptive features of pigmented eggs; dark eggs absorb heat more readily and thus may promote more rapid development, and the melanin may serve to shield the embryos from ultraviolet radiation. The larvae of most of the species of *Leptodactylus* have muscular, thin bodies, probably an adaptation that facilitates migration from the foam nest to adjacent water. Larvae of *L. andreae* develop within the nest; these have not been observed at Santa Cecilia. *Physalaemus petersi* tadpoles have round, robust bodies in contrast to the other leptodactylids, perhaps because the foam nests are produced on the water surface; thus, the tadpoles are not subject to the transient dangers encountered by most *Leptodactylus* larvae.

Five species of frogs (Dendrobatidae) deposit terrestrial eggs; the larvae, upon hatching, are carried to water on the dorsum of the adults. Presently, it is suspected that whether males or females transport the larvae is species-specific, but the suspicion is based on small sample sizes. Only one male *Colostethus marchesianus,* two male *Dendrobates parvulus,* and a female *Phyllobates femoralis* were found transporting tadpoles, but this mode of reproduction is assumed to be similar for the other two species. The snout-vent length of the *C. marchesianus* was 18.5 mm; three tadpoles were found on the dorsum, ranging from 8.0 to 8.5 mm in total length. The snout-vent lengths of the *D. parvulus* were 19.0 and 18.5 mm; the first carried six tadpoles (12.0 to 13.0 mm) and the second, five larvae (not measured). The female *P. femoralis* was 25.5 mm in snout-vent length and carried 11 tadpoles (9.0 to 11.0 mm). The four adults had no apparent (visible) modifications on the dorsal surface for attachment of the larvae. The larval body form is depressed slightly, and the anteroventral half of the tadpole is slightly concave in each species. This shape probably facilitates the larva's fitting onto the slightly curved surface of the adult's dorsum. The tail is sturdy and the tail fin relatively shallow.

Several investigators have described adaptations in other dendrobatids. Ruthven and Gaige (1915) discussed the breeding habits of a frog identified as *Prostherapis* (= *Colostethus*) *subpunctatus.* They thought the tadpoles were attached to the adult by their lips. Likewise, Barbour (1926) stated that the larvae of several species of *Phyllobates* and *Dendrobates* adhere to the adult by "sucker-like mouths." No other suggestions of oral adaptations have been reported. Stebbins and Hendrickson (1959) studied the tadpole-carrying habit of a dendrobatid identified as *Phyllobates* (= *Colostethus*) *subpunctatus* from near Bogotá, Colombia. They stated that the tadpoles were attached to the back of the adult frog by a sticky mucus, probably from dermal glands of the adult. I observed no trace of mucus on any animals from Santa Cecilia, nor has Stephen R. Edwards (personal communication) observed any on individuals of many species of *Colostethus.* The tadpoles are capable of maintaining their position on the dorsum in spite of considerable physical disturbance. Release seems to be a combination of larval and adult activity, and is probably correlated with larval age and the activity of the adult in relation to the physical environment. It is unknown how the larvae initially become situated on the dorsum of the adult.

Fourteen species of frogs (genus *Eleutherodactylus*) deposit large, nonaquatic eggs in which development takes place within the egg capsule, resulting in the hatching of a miniature replica of the adult. The eggs are non-pigmented and protected by several dense jelly layers. Noble (1931) described the tails of the developing embryos as broad and thin; the dorsal and ventral fins are highly vascularized, presumably to act as the respiratory organ for the embryo during the intraoval development. Hatchling *Eleutherodactylus* have a horny projection ("egg tooth") on the tip of the

snout used in ripping the jelly capsule during hatching. The "egg tooth" is shed soon after hatching.

No adult female *Hemiphractus proboscideus* with eggs or young attached, or with evidence of previous attachment, has been found. This reproductive mode is documented in the other four species of *Hemiphractus* (Trueb, 1974); the method of attachment is expected to be the same in *H. proboscideus* as in *Hemiphractus panamensis*, in which the eggs are carried in separate depressions on the dorsum of the female. Development is completed within the egg. Duellman (1970) described the method of attachment of young *H. panamensis* to the adult female. The gills of each juvenile frog are embedded in pits on the dorsum of the female; two pairs of white cords extend from the gills to the throat of the young frog. Noble (1917) did histologic examinations of the gills of hatchling froglets. He showed that the cords contain blood vessels and striated muscle and that the blood vessels anastomose in the gills. Because the gills apparently are separated from vascular tissue in the female, the developing frogs probably do not derive nourishment or oxygen from the parent. Duellman (1970) suggested that the gills serve to obtain oxygen from the atmosphere and to provide firm attachment to the female for transportation.

BREEDING SITE UTILIZATION

The 74 species observed in the course of field work are considered here to be the Santa Cecilia "anuran community." Community is used in the loose sense, as defined by MacArthur (1971) to be "any set of related organisms living near each other and about which it is interesting to talk." Of prime importance is the question: how are 74 species of frogs able to coexist in so small an area? One possible answer lies in the temporal and spatial partitioning by the animals of environmental resources such as food, breeding sites, and shelter. Shelter sites were not studied for logistic reasons; frogs are difficult to find in their inactive periods, and species are encountered with differential success. Stomach content analyses indicate that the majority of the species are opportunistic feeders; there is extensive overlap of prey items. For the present study, I assume that abundance of prey items did not significantly limit the spatial and temporal distribution of breeding activities of the 74 species. The premise of this study is that breeding sites represent a potentially limiting resource, because "X number of aquatic environments is less than "N" number of species. There may be competition for space either in the tadpole stage or in the adult stage, at egg deposition sites. If this is true, differential spatial and temporal utilization of the sites should exist.

Spatial Utilization

Breeding habitats and egg deposition sites for all of the 81 species are listed in Appendix 1. The 14 species of *Eleutherodactylus* deposit eggs either on the ground amidst leaf litter or in vegetation above ground. Because these microenvironments are structurally complex, breeding sites probably are not limited for these species. *Leptodactylus andreae* produces foam nests on the ground in humid places away from open bodies of water. Presumably, *Hemiphractus proboscideus* exhibits complete parental care with the eggs and young being carried on the dorsum of the female. *Hyla boans* constructs nests in the mud along the bank of the Río Aguarico, and *Nyctimantis rugiceps* probably deposits eggs in tree cavities. There is no interspecific overlap in breeding sites for the latter four species.

Of the 74 species, 53 utilize water-filled ditches, puddles, ponds, swamps, a lake, or streams for breeding purposes. Spatial utilization of breeding sites was studied to determine whether the species demonstrate regular or clumped distributions among the available sites with regard to breeding activities.

None of any of the species for which the breeding sites are known is distributed regularly within the habitats. The three major environments are forest, forest-edge and open, disturbed areas. Some species are habitat specialists, breeding in a restricted variety of sites. *Hyla geographica,* for example, breeds only at the large, permanent lake. Many species of tree frogs are habitat generalists, breeding in all three major environments. However, no species was found breeding at each of the eight sites studied in the three environments.

Biotic interactions with other species may prevent a species from breeding at a site even when physical conditions are appropriate. For example, *Hyla triangulum* breeds at both of the open area sites and both forest-edge swamps, but only at one of the forest sites. Distance of the forest site from the clearing probably is not the reason that individuals do not breed at the three sites because two of the swamps are closer to the clearing than is the lake. The amount of open water and density of surrounding vegetation do not seem to be restricting factors because the species breeds in a wide variety of habitats (from shallow water in low, grassy vegetation to the large lake with minimal peripheral vegetation). The species also breeds in ephemeral, temporary, and permanent water. The most parsimonious explanation is that Heliconia Swamp, Palm Pond, and Second-growth Forest Swamp are already "packed" with species, inhibiting the presence of *Hyla triangulum.* The proximate factor may be acoustical interaction, competition for calling or breeding sites, or a combination of these factors. Thus, there seems to be a definite pattern to species distributions, resulting from physical requirements and biotic interactions, with the net result being spatial partitioning of the breeding sites.

In order to elucidate this partitioning, eight aquatic breeding sites and 26 associated species with aquatic larvae were studied in detail (Table 2). Two sites were in disturbed areas, two at the edge of forest, and four in forest. Heliconia Swamp, located in the forest, had the largest number of species (22) associated with it. Of these, only 16 were found calling and/or breeding. Temporal utilization was studied extensively at this site and is discussed in the following section. Two of the forest sites had relatively few species associated with them. Only four species were found actually calling and/or breeding at the lake and eight at the second-growth forest swamp. It is interesting to note that these permanent sites (also with deep water) have the fewest species breeding at them. Seventeen species were found at the fourth forest swamp (Palm Pond), 15 of which were calling and/or breeding. The disturbed area and forest-edge sites had similar numbers of species with 16 and 19 at the former and 19 and 15 at the latter sites. The numbers of species calling and/or breeding were 13, 15, 16, and 15, respectively. In several cases, although calling males were found, no gravid females, eggs, or tadpoles attributable to the species were observed. The maximum number of species breeding at any site was 14 (of 53 potential species); the maximum number of species breeding synchronously at a given site was ten (see below).

These eight sites then were assessed for number of shared species actually breeding for every habitat combination (Table 3). The water-filled ditches along the edge of the runway had no species in common with Second-growth Forest Swamp. Superficially, this seems anomalous because the sites are in close proximity (Fig. 3). However, the vegetational physiognomy and water depth at the two sites are drastically different. The former has shallow, ephemeral water, choked with low, dense, grassy vegetation, whereas the latter is a deep, permanent pond, with large peripheral vegetation. The species involved may be specialized to the water depth, temperature, turbidity, certain chemical properties, amount of open water, or

TABLE 2.—COMPARISONS FOR SPECIES WITH AQUATIC LARVAE OF EIGHT AQUATIC BREEDING SITES ON WHICH THE COMMUNITY MATRICES ARE BASED.[1]

	Air Strip Edge Ditches (A.S.E.D.)	Clearing Swamp (C.S.)	Forest Edge Swamp A (F.E.S.A.)	Forest Edge Swamp B (F.E.S.B.)	Heliconia Swamp (H.S.)	Second-Growth Forest Swamp (S.G.F.S.)	Palm Pond (P.P.)	Lake (L.)
Habitat	Open, disturbed	Open, disturbed	Forest-edge	Forest-edge	Forest	Forest	Forest	Forest
Approx. Dimensions	5-20 × < 1 m.	12 × 5 m.	15 × 7 m.	8 × 5 m.	50 ×15 m.	70 × 15 m.	100 × 30 m.	300 × 100 m.
Permanence	Ephemeral	Temporary	Temporary	Temporary	Temporary	Permanent	Permanent	Permanent
Total # Species Found Within 3 m. of H_2O	16	19	19	15	22	11	17	11
Total # Species Found Calling and/ or Breeding	13	15	16	15	16	8	15	4
Total # Species Breeding	9	10	14	13	12	7	13	4
Max. # Species Calling and/or Breeding Synchronously	9	11	8	9	10	6	12	4
Max. # Species Breeding Synchronously	5	5	6	5	6	3	10	2

[1] In addition to the 26 species listed in Appendix 2, eight other species are included because they were found within 3 m. of the sites, although no breeding activity was observed.

TABLE 3.—MATRIX OF SIMILARITY COEFFICIENTS FOR EIGHT AQUATIC SITES BASED ON SHARED SPECIES BREEDING AT THE SITES.[1]

	A.S.E.D.	C.S.	F.E.S.A.	F.E.S.B.	H.S.	S.G.F.S.	P.P.	L.
A.S.E.D.	X							
C.S.	6(0.46)	X						
F.E.S.A.	5(0.28)	7(0.41)	X					
F.E.S.B.	7(0.47)	7(0.44)	9(0.50)	X				
H.S.	2(0.11)	4(0.22)	9(0.53)	8(0.47)	X			
S.G.F.S.	0(0.00)	3(0.21)	4(0.24)	2(0.11)	3(0.19)	X		
P.P.	1(0.05)	5(0.28)	7(0.35)	6(0.30)	9(0.56)	4(0.25)	X	
L.	1(0.08)	1(0.08)	1(0.06)	1(0.06)	0(0.00)	2(0.22)	0(0.00)	X
Total Species Breeding	9	10	14	13	12	7	13	4

[1] The sites are as follows: Air Strip Edge Ditches, ASED; Clearing Swamp, CS; Forest Edge Swamp A, FESA; Forest Edge Swamp B, FESB; Heliconia Swamp, HS; Second-Growth Forest Swamp, SGFS; Palm Pond, PP; Lake, L. See Appendix 3 for raw data. In each column the first figure indicates the number of shared species; the figure in parentheses is the similarity coefficient.

some other variable. The maximum number of shared species between two sites is 9, exhibited between two forest swamps (Heliconia Swamp and Palm Pond), two forest-edge swamps (A and B), and between one forest and one forest-edge swamp (Heliconia Swamp and Forest Edge Swamp A). The highest similarity coefficient (taking into consideration both total numbers of species at each site and number of shared species) is 0.56, between the two forest swamps. Thus, 56 per cent of all the species found breeding at either site are found breeding at both sites.

The preceding data indicate that spatial partitioning does exist. The range of similarity coefficients representing species associations at the eight breeding sites is 0-1 (Table 4), which means that some species combinations never were found breeding at the same sites, whereas other pairs always were found in mutual association. It is assumed that the higher the similarity coefficient, the more similar are the requirements for breed-

TABLE 4.—COMMUNITY MATRIX OF SIMILARITY COEFFICIENTS OF 26 SPECIES OF FROGS BREEDING AT EIGHT SITES.

Species	1	2	3	4	5	6	7	8	9	10
1	X	0.33	0.20	0.20			0.33	0.20	0.60	
2	0.33	X		0.33					0.20	
3	0.20		X	0.20	0.33		0.60	1	0.33	
4	0.20	0.33	0.20	X	0.33		0.14	0.20	0.33	
5			0.33	0.33	X		0.20	0.33		
6						X	0.17			0.50
7	0.33		0.60	0.14	0.20	0.17	X	0.60	0.43	
8	0.20		1	0.20	0.33		0.60	X	0.33	
9	0.60	0.20	0.33	0.33			0.43	0.33	X	
10						0.50				X
11						1	0.17			0.50
12	0.75	0.25	0.17	0.40			0.29	0.17	0.80	
13	0.50	0.33	0.20	0.20			0.33	0.20	0.60	
14	0.40		0.75	0.17	0.25		0.80	0.75	0.50	
15			0.20	0.50	0.33	0.25	0.33	0.20	0.14	
16	0.29		0.50	0.29	0.17	0.14	0.83	0.50	0.57	
17	0.75	0.25	0.17	0.40			0.29	0.17	0.80	
18	0.50	0.33		0.50			0.14		0.60	
19	0.14		0.60	0.33	0.20	0.17	0.67	0.60	0.43	
20	0.25		0.67				0.40	0.67	0.40	

TABLE 4.—COMMUNITY MATRIX OF SIMILARITY COEFFICIENTS OF 26 SPECIES OF FROGS BREEDING AT EIGHT SITES.—*Continued.*

Species	1	2	3	4	5	6	7	8	9	10
21	0.25		0.25			0.33	0.40	0.25	0.17	
22	0.33		0.60	0.33	0.20		0.67	0.60	0.67	
23	0.60	0.20	0.14	0.33		0.17	0.25	0.14	0.67	0.20
24	0.20		0.50	0.20	0.33		0.60	0.50	0.33	
25	0.20		0.50	0.20	0.33		0.60	0.50	0.33	
26			0.33	0.33	1		0.20	0.33		

Species	11	12	13	14	15	16	17	18	19	20
1		0.75	0.50	0.40		0.29	0.75	0.50	0.14	0.25
2		0.25	0.33				0.25	0.33		
3		0.17	0.20	0.75	0.20	0.50	0.17		0.60	0.67
4		0.40	0.20	0.17	0.50	0.29	0.40	0.50	0.33	
5				0.25	0.33	0.17			0.20	
6	1				0.25	0.14			0.17	
7	0.17	0.29	0.33	0.80	0.33	0.83	0.29	0.14	0.67	0.40
8		0.17	0.20	0.75	0.20	0.50	0.17		0.60	0.67
9		0.80	0.60	0.50	0.14	0.57	0.80	0.60	0.43	0.40
10	0.50									
11	X				0.25	0.14			0.17	
12		X	0.40	0.33	0.17	0.43	1	0.75	0.29	0.20
13		0.40	X	0.40		0.29	0.40	0.50	0.14	0.25
14		0.33	0.40	X	0.17	0.67	0.33	0.17	0.50	0.50
15	0.25	0.17		0.17	X	0.50	0.17	0.20	0.60	
16	0.14	0.43	0.29	0.67	0.50	X	0.43	0.29	0.83	0.33
17		1	0.40	0.33	0.17	0.43	X	0.75	0.29	0.20
18		0.75	0.50	0.17	0.20	0.29	0.75	X	0.14	
19	0.17	0.29	0.14	0.50	0.60	0.83	0.29	0.14	X	0.40
20		0.20	0.25	0.50		0.33	0.20		0.40	X
21	0.33	0.20		0.20	0.25	0.33	0.20		0.40	0.33
22		0.50	0.33	0.80	0.33	0.83	0.50	0.33	0.67	0.40
23	0.17	0.80	0.33	0.29	0.14	0.38	0.80	0.60	0.25	0.17
24		0.17	0.50	0.75	0.20	0.50	0.17	0.20	0.33	0.25
25		0.17	0.50	0.75	0.20	0.50	0.17	0.20	0.33	0.25
26				0.25	0.33	0.17			0.20	

Species	21	22	23	24	25	26	No. Sites	Pot. Assoc.[1]	Σ Coef.
1	0.25	0.33	0.60	0.20	0.20		3	19	7.02
2			0.20				1	8	2.22
3	0.25	0.60	0.14	0.50	0.50	0.33	3	20	8.24
4		0.33	0.33	0.20	0.20	0.33	3	20	5.91
5		0.20		0.33	0.33	1	1	12	4.00
6	0.33		0.17				2	8	2.73
7	0.40	0.67	0.25	0.60	0.60	0.20	5	23	9.44
8	0.25	0.60	0.14	0.50	0.50	0.33	3	20	8.24
9	0.17	0.67	0.67	0.33	0.33		5	20	9.23
10			0.20				1	3	1.20
11	0.33		0.17				2	8	2.73
12	0.20	0.50	0.80	0.17	0.17		4	20	8.24
13		0.33	0.33	0.50	0.50		3	18	6.40
14	0.20	0.80	0.29	0.75	0.75	0.25	4	21	9.73
15	0.25	0.33	0.14	0.20	0.20	0.33	3	20	5.46
16	0.33	0.83	0.38	0.50	0.50	0.17	6	23	9.91
17	0.20	0.50	0.80	0.17	0.17		4	20	8.24
18		0.33	0.60	0.20	0.20		3	16	6.20
19	0.40	0.67	0.25	0.33	0.33	0.20	5	23	8.68

[1] Entries under the heading "Pot. Assoc." represent the total number of potential species associations (number of species found breeding sympatrically).

TABLE 4.—COMMUNITY MATRIX OF SIMILARITY COEFFICIENTS OF 26 SPECIES OF FROGS BREEDING AT EIGHT SITES.—*Continued.*

Species	21	22	23	24	25	26	No. Sites	Pot. Assoc.[1]	Σ Coef.
20	0.33	0.40	0.17	0.25	0.25	-----	2	16	5.67
21	X	0.17	0.17	-----	-----	-----	2	16	4.23
22	0.17	X	0.43	0.60	0.60	0.20	5	21	10.09
23	0.17	0.43	X	0.14	0.14	-----	5	23	7.51
24	-----	0.60	0.14	X	1	0.33	3	20	7.80
25	-----	0.60	0.14	1	X	0.33	3	20	7.80
26	-----	0.20	-----	0.33	0.33	X	1	12	4.00

ing. The number of breeding sites per species ranges from one to six.

TEMPORAL UTILIZATION

The next relevant questions are: how are these eight sites partitioned in time, and how do the actual species associations compare with the potential associations? A "potential association" is one in which two species breed at the same site; an "actual association" is one in which the species breed at the same site at the same time. As indicated, the maximum number of species breeding at one place synchronously was ten, at Palm Pond. The next largest number was 6, at both Heliconia Swamp and Forest Edge Swamp A. When temporal characteristics are superimposed onto the data from table 4 concerning potential species associations, further partitioning of the breeding sites is evident. Table 5 indicates that many potential species interactions do not occur, due to temporal partitioning. The most extreme cases are those of *Hyla funerea* and *Hyla brevifrons,* in which 45 and 50 per cent, respectively, of their potential species associations do not occur due to temporal segregation. On the other hand, *Bufo marinus* and *Hyla geographica* breed with their associated species throughout the year; perhaps this is explained partially by the fact that both species breed with relatively few other species. Spatial utilization was studied for 26 species; the number of potential species associations not found breeding synchronously ranged from 0 to 11, with a mean of 4.0 species. Temporal segregation probably results from both interspecific competition and differential response to external stimuli.

Because closely related species often have similar ecological requirements, it is meaningful to study species groups in order to determine the amount of interspecific overlap and segregation of habitat. Breeding activities of the following species groups of *Hyla* at the eight sites were analyzed to determine extent of spatial and temporal segregation: (1) *leucophyllata* group—*H. bifurca, H. favosa, H. leucophyllata, H. sarayacuensis,* and *H. triangulum;* (2) *parviceps* group —*H. bokermanni, H. brevifrons,* and *H. parviceps;* and (3) *rubra* group—*H. cruentomma, H. funerea, H. garbei,* and *H. rubra.* Segregation is maximal in the *leucophyllata* group, in which only three of the five species were observed to breed sympatrically and synchronously. These species frequently did so at several sites. Three of the four species of the *rubra* group were found together, but only infrequently. All three members of the *parviceps* group were observed breeding sympatrically only once, but *H. bokermanni* and *H. brevifrons* were found breeding individually in association with *H. parviceps* on many occasions.

Heliconia Swamp.—Throughout the year considerable time was spent at Heliconia Swamp studying use of the environment for breeding activities (Table 6). Twenty-five species were found at the site. Three of these have direct development (*Eleutherodactylus croceoinguinis, E. quaquaversus,* and *E. varia-*

TABLE 5.—Community Matrix of Species Breeding Sympatrically and Synchronously.[1]

Species	Species 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	E No.	E %
1	X	+	-	+	N	N	+	-	+	N	N	+	+	+	N	+	+	+	+	+	+	+	+	+	+	N	0.40	5.70
2	+	X	N	+	N	N	N	N	+	N	N	+	+	N	N	N	+	+	N	N	N	N	+	N	N	N	0.00	---
3	-	N	X	-	+	N	+	+	-	N	N	-	-	+	+	+	+	N	+	+	+	+	-	+	+	+	1.07	12.99
4	+	+	-	X	-	N	-	-	+	N	N	+	+	-	+	+	+	+	-	N	N	+	+	-	-	-	2.10	35.53
5	N	N	+	-	X	N	+	-	N	N	N	N	N	+	+	+	N	N	+	N	N	+	N	+	+	+	0.66	16.50
6	N	N	N	N	N	X	-	N	N	+	+	N	N	N	+	-	N	N	-	N	+	N	+	N	N	N	0.48	17.58
7	+	N	+	-	+	-	X	+	+	N	-	-	+	+	+	+	+	-	+	+	+	+	-	+	+	+	1.16	12.29
8	-	N	+	-	-	N	+	X	-	N	N	-	-	+	+	+	-	N	+	-	-	+	-	+	+	-	2.99	36.29
9	+	+	-	+	N	N	+	-	X	N	N	+	+	+	+	+	+	+	+	-	-	+	+	+	+	N	1.23	13.33
10	N	N	N	N	N	+	N	N	N	X	+	N	N	N	N	N	N	N	N	N	N	N	+	N	N	N	0.00	---
11	N	N	N	N	N	+	-	N	N	+	X	N	N	N	-	-	N	N	+	N	+	N	+	N	N	N	0.56	20.51
12	+	+	-	+	N	N	-	-	+	N	N	X	+	+	+	+	+	+	+	-	-	+	+	-	-	N	1.37	16.63
13	+	+	-	+	N	N	+	-	+	N	N	+	X	+	N	+	+	+	-	-	N	+	+	+	+	N	0.79	12.34
14	+	N	+	-	+	N	+	+	+	N	N	+	+	X	+	+	+	-	+	+	-	+	+	+	+	+	0.54	5.55
15	N	N	+	+	+	+	+	+	+	N	-	+	N	+	X	+	+	+	+	N	+	+	+	+	+	+	0.25	4.58
16	+	N	+	+	+	-	+	+	+	N	-	+	+	+	+	X	+	+	+	+	+	+	+	+	+	+	0.28	2.83
17	+	+	+	+	N	N	+	-	+	N	N	+	+	+	+	+	X	+	+	+	-	+	+	+	+	N	0.37	4.49
18	+	+	N	+	N	N	-	N	+	N	N	+	+	-	+	+	+	X	-	N	N	+	+	+	+	N	0.45	7.26
19	+	N	+	-	+	-	+	+	+	N	+	+	-	+	+	+	+	-	X	+	+	+	-	+	+	+	1.03	11.87
20	+	N	+	N	N	N	+	-	-	N	N	-	-	+	N	+	+	N	+	X	+	-	-	-	-	N	2.59	45.68
21	+	N	+	N	N	+	+	-	-	N	+	-	N	-	+	+	-	N	+	+	X	-	-	N	N	N	1.36	32.15
22	+	N	+	+	+	N	+	+	+	N	N	+	+	+	+	+	+	+	+	-	-	X	+	+	+	+	0.57	5.65
23	+	+	-	+	N	+	-	-	+	+	+	+	+	+	+	+	+	+	-	-	-	+	X	+	+	N	1.12	14.91
24	+	N	+	-	+	N	+	+	+	N	N	-	+	+	+	+	+	+	+	-	N	+	+	X	+	N	0.62	7.95
25	+	N	+	-	+	N	+	+	+	N	N	-	+	+	+	+	+	+	+	-	N	+	+	+	X	+	0.62	7.95
26	N	N	+	-	+	N	+	-	N	N	N	N	N	+	+	+	N	N	+	N	N	+	N	+	+	X	0.66	16.50
A/P Ratio	17/19	8/8	14/20	11/20	10/12	5/8	17/23	9/20	16/20	3/3	5/8	13/20	14/18	18/21	19/20	21/23	18/20	13/16	18/23	8/16	9/16	19/21	17/23	17/20	17/20	10/12		
%	89.5	100	70.0	55.0	83.3	62.5	73.9	45.0	80.0	100	62.5	65.0	77.8	85.7	95.0	91.3	90.0	81.3	79.3	50.0	56.3	90.5	73.9	85.0	85.0	83.3		

[1] See Appendix 2 for species names and Table 4 for similarity coefficients for the species. An "N" indicates the two species were never found breeding at the same site. A "+" indicates the two species were found breeding sympatrically and synchronously; a "—" indicates the breeding of the two species was segregated temporally. "A/P" indicates the ratio of actual species associations to potential species associations. "E" indicates potential species interactions eliminated due to temporal segregation.

TABLE 6.—OCCURRENCE AND BREEDING ACTIVITY[1] OF 20 SPECIES AT HELICONIA SWAMP.

Species	20-Day Time Period 1	2	3	4	5	6	7	8	9	10
H. alboguttata	-----	G	G	M	F	F	-----	-----	-----	-----
H. bokermanni	GC	-----	-----	-----	-----	GC	GC	GC	-----	M
H. brevifrons	-----	-----	M	-----	-----	M	-----	-----	-----	-----
H. calcarata	-----	-----	-----	-----	-----	-----	F	-----	-----	-----
H. cruentomma	C	-----	-----	-----	M	C	-----	-----	-----	C
H. favosa	-----	-----	-----	-----	-----	-----	M	-----	-----	-----
H. funerea	-----	-----	-----	-----	M	-----	-----	-----	-----	M
H. garbei	-----	GC	-----	-----	-----	C	GC	C	-----	GC
H. geographica	FM	FM	-----	-----	-----	-----	-----	-----	-----	-----
H. leucophyllata	-----	-----	-----	-----	-----	-----	C	-----	-----	-----
H. marmorata	-----	-----	-----	-----	-----	-----	-----	-----	-----	GC
H. parviceps	-----	GC	-----	-----	-----	GC	GC	GC	-----	GC
H. rhodopepla	GC	GC	-----	-----	-----	GC	GC	GC	-----	GC
H. sarayacuensis	C	C	-----	M	C	C	GC	-----	-----	M
P. palliata	-----	C	-----	-----	-----	C	C	GC	-----	C
P. tarsius	C	-----	-----	-----	C	GC	-----	-----	-----	-----
C. ventrimaculata	-----	-----	-----	-----	-----	-----	-----	-----	-----	C
H. boliviana	-----	-----	-----	-----	-----	C	M	-----	-----	C
L. mystaceus	-----	-----	C	-----	C	C	-----	-----	-----	-----
L. pentadactylus	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Water Depth (ft.)	1.5-2.0	2.0	Dry	Dry	Dry-1.0	1.0-1.5	2.0-2.5	2.5	1.5	1.5-2.0
Tot. No. Species Breeding	2	4	1	0	0	4	5	4	0	4

Species	20-Day Time Period 11	12	13	14	15	16	17	18	19	20
H. alboguttata	-----	-----	-----	-----	C	-----	-----	-----	-----	-----
H. bokermanni	-----	-----	GC	GC	GC	-----	GC	-----	C	C
H. brevifrons	-----	-----	GC	-----	-----	-----	-----	-----	-----	-----
H. calcarata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
H. cruentomma	-----	-----	-----	GC	-----	-----	C	-----	-----	GC
H. favosa	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
H. funerea	-----	-----	-----	-----	-----	-----	-----	-----	-----	GC
H. garbei	-----	-----	-----	C	-----	-----	-----	-----	-----	GC
H. geographica	-----	-----	F	-----	-----	-----	-----	-----	-----	F
H. leucophyllata	-----	-----	C	C	-----	-----	C	-----	-----	-----
H. marmorata	-----	-----	-----	-----	-----	-----	-----	-----	C	-----
H. parviceps	-----	-----	C	GC	-----	-----	C	-----	GC	GC
H. rhodopepla	-----	-----	GC	GC	-----	-----	GC	-----	GC	GC
H. sarayacuensis	-----	-----	GC	GC	C	-----	GC	-----	C	C
P. palliata	-----	C	GC	C	C	-----	C	-----	C	C
P. tarsius	-----	C	C	GC	GC	-----	C	-----	-----	C
C. ventrimaculata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
H. boliviana	-----	-----	-----	-----	-----	-----	C	-----	-----	C
L. mystaceus	-----	-----	C	-----	C	-----	-----	-----	-----	-----
L. pentadactylus	-----	-----	-----	F	-----	-----	-----	-----	-----	-----
Water Depth (ft.)	Dry	Dry-0.5	Dry-1.0	2.5-3.0	1.0	Dry	1.5	1.0	1.0-1.5	3.0
Tot. No. Species Breeding	0	0	5	6	3	0	3	0	2	5

[1] Symbols: non-gravid female(s), F; gravid female(s), G; non-calling male(s), M; calling male(s), C.

bilis), and two are dendrobatids (*Dendrobates pictus* and *Colostethus marchesianus*); no breeding activities were observed for these species. Non-gravid females of *Hyla calcarata*, *H. geographica*, and *Leptodactylus pentadactylus* occasionally were found at the swamp; these species are excluded from the discussion, because no calling males were observed. One male *Hyla favosa* was found, but no females. Males of each of the remaining 16 species, with the exception of *Hyla alboguttata*, were found calling. Gravid females of 12 of these species were found.

Thus, it is probable that at least 16 species breed in the swamp. The maximum number of species observed calling at one time was ten. However, the maximum number of species observed breeding synchronously was six. Of these, three deposit eggs on vegetation above water (*Hyla bokermanni*, *H. sarayacuensis*, and *Phyllomedusa tarsius*), and three deposit eggs directly in water (*Hyla cruentomma*, *H. parviceps*, and *H. rhodopepla*), thereby creating less demand on potentially limited oviposition sites. Three species (*H. bokermanni*, *H. parviceps*, and *H. rhodopepla*) almost always were found breeding following heavy rains. Others (*Hyla garbei*, *H. sarayacuensis*, *Phyllomedusa palliata*, and *P. tarsius*) bred occasionally at the swamp. *Hyla garbei* bred only when there was at least 0.6 m of water in the swamp. The cyclic patterns of the other species are unexplainable in the absence of detailed environmental measurements, but they seem less affected by the physical environment than by interspecific associations. Both species of *Phyllomedusa* often were found calling synchronously, but gravid females or egg clutches of only one species were found during any 20-day period.

Herpetologists have suggested that on any given night the most abundant species calling and/or breeding at a site will be the one that arrives first and begins vocalizing, attracting other males. Perhaps this explains the presence or absence of certain species at Heliconia Swamp at a particular time. Occasionally, species calling and breeding in abundance at sites less than a kilometer from the swamp were absent from Heliconia Swamp, yet on the preceding and following nights individuals of the species were breeding in great abundance there. No differences in climatic factors or the physical environment were detected. Therefore, I suggest that the presence and absence of species is at least partly related to the existing biotic associations. Although at times *H. bokermanni* was the most abundant species, at other times *H. rhodopepla* was more abundant. But sometimes both species were calling and breeding in such abundance that it was impossible to single out one as dominant with the data at hand. No one species within the community can be identified as the reason for another's absence. If competitive interactions are important, a synergistic interaction of numerous species is probably responsible for the presence and absence of certain species at a particular breeding site at a given time.

Annual Breeding Patterns.—Within the anuran community at Santa Cecilia, it is possible to discern distinct annual breeding patterns. I have grouped the species into three categories on the basis of annual reproductive activity—continuous breeders, opportunistic breeders, and sporadic breeders (Table 7). A species is designated a continuous breeder if gravid females and/or juveniles were found throughout the year. Appendix 4 indicates the number of females and the per cent gravid females found per 20-day time period. At least ten species are continuous breeders. Others probably should be included in this group, but more data are necessary to verify this conclusion. For example, male *Leptodactylus mystaceus* were found calling throughout the year, but only 16 gravid females were found (in July, October, November, January, February, March, and May).

Eight hylids are classified as oppor-

TABLE 7.—BREEDING PATTERNS OF 49 SPECIES OF FROGS AT SANTA CECILIA.[1]

Continuous	Opportunistic	Wet	Sporadic Dry	Environmental Factor Unknown
Eleutherodactylus croceoinguinis	*Hyla bifurca*	*Bufo marinus*	*Leptodactylus pentadactylus*	*Eleutherodactylus acuminatus*
Eleutherodactylus lanthanites	*Hyla bokermanni*	*Hyla cruentomma*	*Hyla boans*	*Eleutherodactylus altamazonicus*
Eleutherodactylus variabilis	*Hyla brevifrons*	*Hyla funerea*		*Eleutherodactylus conspicillatus*
Bufo typhonius	*Hyla marmorata*	*Hyla granosa*		*Eleutherodactylus lacrimosus*
Dendrophryniscus minutus	*Hyla rhodopepla*	*Hyla leucophyllata*		*Eleutherodactylus martiae*
Dendrobates parvulus	*Hyla rubra*	*Hyla punctata*		*Eleutherodactylus ockendeni*
Hyla fasciata	*Hyla sarayacuensis*	*Osteocephalus leprieurii*		*Eleutherodactylus pseudoacuminatus*
Hyla garbei	*Hyla triangulum*	*Phyllomedusa palliata*		*Leptodactylus andreae*
Hyla lanciformis		*Phyllomedusa tarsius*		*Hyla alboguttata*
Hyla parviceps		*Phyllomedusa tomopterna*		*Hyla calcarata*
Probably Continuous		*Phyllomedusa vaillanti*		*Hyla geographica*
Ischnocnema quixensis				*Hamptophryne boliviana*
Leptodactylus mystaceus				
Colostethus marchesianus				
Dendrobates pictus				
Phyllobates femoralis				
Rana palmipes				
16 Species	8 Species		25 Species	

[1] Pattern is unknown for the 25 additional species at Santa Cecilia.

tunistic breeders. These frogs breed regularly following heavy rains, at which time they use ephemeral and temporary ponds and ditches filled with water.

Twenty-five species are classified as sporadic breeders. *Hyla boans* and *Leptodactylus pentadactylus* breed during drier periods. Many hylids and *Bufo marinus* breed after heavy rains, but sporadically rather than regularly. The environmental conditions stimulating reproduction are unclear for 12 species; gravid females were abundant both during dry and wet periods. These species are not dependent upon the filling of small, temporary bodies of water; the group includes seven species of *Eleutherodactylus* (terrestrial or arboreal eggs), *Leptodactylus andreae* (foam nest on land), *Hamptophryne boliviana* (breeds in relatively large forest ponds and swamps), *Hyla calcarata* (perma-

nent forest swamp and stream), *Hyla geographica* (lake), and *Hyla alboguttata* (breeding site unknown).

The remaining 25 species were found too infrequently to discern breeding patterns.

Females of 17 species were abundant throughout the year (30 or more individuals found). For these species, at least 55 per cent of all females found contained mature ovarian eggs (Appendix 4). Eight are species that deposit eggs directly in water. Only 55.4 per cent of all female *Dendrophryniscus minutus* contained mature ovarian eggs, whereas 98.2 per cent of the *Hyla rhodopepla* were gravid with mature eggs. For these eight species, the mean percentage of females found to be gravid was 79.2. *Hyla bokermanni* and *Hyla triangulum* are the only species depositing eggs on vegetation above water for which females were found in abundance; 92.4 per cent of the former species and 90.0 per cent of the latter contained mature ovarian eggs. Nearly all female dendrobatids were gravid; the percentage gravid of the three most abundant species was 92.3, 93.0, and 96.4. Of the 14 species of *Eleutherodactylus*, females of only four species were found in abundance; the range of females containing mature ovarian eggs was 60.0 to 88.9 per cent.

Many of these percentages seem suspiciously high. Among the hylids this is explained by the fact that females were usually found at aquatic breeding sites. Females generally do not come to the site until they are ready to deposit eggs. The low percentage of gravid *Hyla alboguttata* is consistent with the fact that individuals were found scattered throughout the forest, rather than at breeding sites. The figures for the dendrobatids may be biased in one or both of two ways—since at least 50 per cent of the dendrobatids seen escaped, females laden with mature eggs are possibly easier to capture, and, possibly, while their eggs are developing, females take shelter in secluded microhabitats. Gravid females were found both on the ground amidst leaf litter by day and sleeping on vegetation up to 0.5 m from the ground at night. The few non-gravid individuals were found in the same habitats.

I have no data concerning the number of times individual females breed annually. However, indirect evidence suggests that females of each reproductive mode (with the possible exception of the species that deposits eggs in tree cavities and those two species in which the eggs and young are attached to the back of the female) lay multiple clutches, throughout the year. All of these females contained immature eggs in addition to the mature ovarian complement. It is unlikely that all of these undeveloped eggs are wasted; the most parsimonious explanation is that they are deposited at some later date. Direct evidence for multiple clutches does exist for one female *Hyla rhodopepla*. A marked individual deposited 390 eggs in May 1972. She was released the following day and recaptured 31 days later; at this time she deposited another 260 eggs. Both clutches were fertilized and subsequently hatched.

QUANTITATIVE REPRODUCTIVE VARIABLES

Certain reproductive factors are quantifiable (size-fecundity and volumetric relationships, sexual dimorphism in size, ovum diameter, intraoval developmental time, and hatchling size); when examined within and between both species and modes of reproduction, analysis of these factors enhances our understanding of anuran reproductive strategies and their evolutionary and ecological significance. Either as a means of or as a result of coexistence, species do partition breeding and oviposition sites temporally and spatially (preceding section). The following section demonstrates that no two species possess an identical complement of reproductive characteristics.

Size-Fecundity Relationships

Snout-vent lengths were measured and mature ovarian egg complements counted for all species for which gravid females were found. Ranges and means of these variables, maximum ova diameters (nearest 0.5 m), and ovarian size factors are listed in table 8.

Several investigators (Henderson, 1961; Oplinger, 1966; Pettus and Angleton, 1967) have shown that as size increases within a species the number of eggs produced increases. In order to determine whether my data show this relationship, product-moment correlation coefficients of ovarian complement on body size were computed for all species having a sample size of at least ten. Both variables were converted to their natural logarithms to reduce curvilinearity and minimize the spread of data points. The data were subsequently re-checked for

Table 8.—Summary of Reproductive Data for 66 Species Based on Mature Ovarian Egg Complement. An asterisk indicates data from Largo Agrio (16 km. from Santa Cecilia).

Species	N	Range SVL	Mean SVL	Range # eggs	Mean # eggs	Max. Egg Diam.	Ovarian size factor
E. perezi	1	38.0	38.0	93	93.0	2.0	4.89
E. acuminatus	5	27.0–31.0	29.2	12–21	18.0	2.5	1.54
E. altamazonicus	20	27.0–31.5	28.1	12–25	18.2	2.5	1.62
E. conspicillatus	10	40.0–44.5	42.3	27–62	42.8	3.5	3.54
E. croceoinguinis	86	18.0–23.0	20.3	2–7	4.8	3.0	0.71
E. diadematus	1	44.5	44.5	43	43.0	2.5	2.42
E. lacrimosus	11	20.0–29.0	23.5	7–16	9.5	2.5	1.01
E. lanthanites	68	34.0–46.0	38.7	20–52	30.4	3.0	2.36
E. martiae	18	19.0–23.0	21.7	5–13	7.8	2.0	0.72
E. ockendeni	29	23.0–29.0	26.4	5–18	13.0	3.0	1.48
E. paululus	1	19.0	19.0	5	5.0	2.5	0.66
E. pseudo-acuminatus	12	18.0–22.0	20.8	4–11	7.3	3.0	1.05
E. quaquaversus	1	29.0	29.0	22	22.0	2.5	1.90
E. variabilis	148	22.0–28.5	24.4	2–11	6.7	3.0	0.82
I. quixensis	34	47.0–62.0	52.9	15–51	35.1	4.0	2.65
L. audreae	12	25.0–29.0	26.7	6–16	8.7	3.0	0.98
L. discodactylus	5	33.0–35.0	33.6	148–420	234.8	1.0	6.99
L. mystaceus	22	52.0–60.0	54.8	171–425	280.5	2.5	12.80
L. wagneri	6	51.0–80.0	68.2	1000–3150	1740.0	1.5	38.27
*L. lineatus**	1	51.0	51.0	195	195.0	2.0	7.65
C. marchesianus	40	16.0–19.0	17.8	7–27	14.0	1.5	1.18
C. sauli	4	24.0–26.0	25.0	6–14	11.0	1.5	0.66
D. parvulus	109	18.5–23.0	21.0	4–16	8.9	3.0	1.27
D. pictus	48	20.5–24.0	22.5	6–31	18.0	2.0	1.60
P. femoralis	12	24.0–28.0	25.6	8–43	22.7	2.0	1.77
H. alboguttata	21	35.0–46.0	41.4	210–870	440.1	1.5	15.95
H. bifurca	8	29.0–35.0	32.9	163–210	186.0	1.5	8.48
H. boans	25	80.0–110.0	99.0	1300–4800	3154.8	2.0	63.73
H. bokermanni	29	22.5–25.5	23.9	65–135	98.3	1.5	6.17
H. brevifrons	15	18.0–23.5	20.9	48–114	79.1	1.0	3.78
H. calcarata	10	47.0–61.0	53.9	835–1600	1143.5	1.5	31.82
H. cruentomma	18	25.0–32.0	28.3	280–1200	580.4	1.0	20.51
H. fasciata	27	45.0–51.0	47.3	360–870	569.1	1.5	18.05
H. favosa	1	40.0	40.0	496	496.0	1.0	12.40
H. funerea	13	33.0–43.0	37.9	225–740	537.8	1.0	14.19
H. garbei	21	39.0–48.0	41.9	280–793	550.8	1.5	19.72
H. geographica	7	64.5–69.0	66.6	1780–4300	2797.1	1.0	42.00
H. granosa	11	40.0–44.0	41.2	350–520	426.4	1.5	15.52

TABLE 8.—SUMMARY OF REPRODUCTIVE DATA FOR 66 SPECIES BASED ON MATURE OVARIAN EGG COMPLEMENT. AN ASTERISK INDICATES DATA FROM LARGO AGRIO (16 KM. FROM SANTA CECILIA).—*Continued.*

Species	N	Range SVL	Mean SVL	Range # eggs	Mean # eggs	Max. Egg Diam.	Ovarian size factor
H. laniformis	23	79.0–94.0	87.3	740–2400	1617.5	2.0	37.06
H. leucophyllata	6	40.0–44.0	42.1	420–910	587.8	1.5	20.94
H. marmorata	7	46.0–53.0	49.3	630–1260	979.4	1.5	29.80
H. minuta	5	23.0–24.0	23.8	160–265	211.6	1.0	8.89
H. parviceps	101	20.0–25.5	23.3	120–395	234.1	1.0	10.05
H. punctata	20	35.0–41.0	37.2	230–430	324.6	1.5	13.09
H. rhodopepla	52	23.0–28.0	26.8	140–422	285.4	1.0	10.65
H. rubra	66	35.0–43.5	39.5	315–960	591.4	1.5	19.80
H. sarayacuensis	14	31.0–37.0	33.6	68–176	113.4	2.0	6.75
H. triangulum	23	36.0–41.5	39.5	320–650	501.7	1.5	19.05
*O. buckleyi**	1	49.0	49.0	580	580.0	1.0	11.84
*O. leprieurii**	16	56.0–64.0	59.8	480–1150	848.1	1.0	14.18
O. taurinus	1	76.0	76.0	550	550.0	1.0	7.24
P. coriacea	1	66.0	66.0	1430	1430.0	2.0	43.33
P. palliata	15	44.0–49.0	46.5	38–106	60.8	2.5	3.27
P. tarsius	15	95.0–111.0	105.3	410–750	548.7	3.0	15.63
P. tomopterna	5	55.0–60.0	57.2	60–89	71.4	3.5	4.37
P. vaillanti	5	68.0–84.0	78.8	912–1250	1114.4	2.0	28.28
S. carneus	1	23.0	23.0	143	143.0	1.0	6.22
C. midas	2	26.0–28.0	27.0	27–29	28.0	1.5	1.56
C. munozorum	1	23.0	23.0	18	18.0	1.5	1.17
C. bassleri	3	25.0–30.0	27.3	151–250	212.0	1.0	7.77
C. ventrimaculata	1	22.0	22.0	210	210.0	1.0	9.55
H. boliviana	2	40.0–44.0	42.0	1370–2186	1788.0	1.0	42.33
B. marinus	5	115.0–146.0	132.6	4240–12700	8598.0	1.5	97.26
B. typhonius	14	54.0–86.5	73.8	310–2500	1537.8	2.0	41.67
D. minutus	41	17.5–22.0	19.1	70–245	150.6	1.0	7.88
R. palmipes	25	103.0–126.0	116.9	720–6750	2859.8	2.0	48.93

normality (Table 9). Only 11 of the 41 species (26.8%) show a significant correlation ($0.05 > P > 0.01$) between size and number of mature ovarian eggs; all are positive correlations: three (18.8%) of 16 species that deposit eggs directly in water; three (37.5%) of eight that deposit eggs on vegetation above water; the one species that constructs nests; one (25.0%) of four that lay terrestrial eggs and carry larvae to water; and three (33.3%) of nine that lay nonaquatic eggs with direct development. Three species have coefficients significant only at $P < 0.1$ (*Ischnocnema quixensis, Phyllobates femoralis,* and *Hyla rubra*), which nonetheless supports a positive relationship between size and fecundity. Thus, within each reproductive mode, less than 40 per cent of the species show a significant correlation ($P < 0.05$) between size and fecundity; these results are contrary to those obtained from studies mentioned above.

The ovarian size factor (see Methods) increases with increasing female size within each reproductive mode; thus, larger species have proportionately much larger egg masses. This index employs the largest ovarian egg diameter of the available sample rather than the mean diameter of deposited eggs.

Salthe and Duellman (1973) demonstrated that within a reproductive mode, larger species produce more eggs. This conclusion was tested by product-moment correlations for three modes at Santa Cecilia—eggs in water, eggs on

TABLE 9.—CORRELATION BETWEEN SNOUT-VENT LENGTH AND NUMBER MATURE OVARIAN EGGS FOR 41 SPECIES OF FROGS.

Species	N	Normality SVL	Normality # eggs	r
E. altamazonicus	11	+	+	0.639°
E. conspicillatus	10	+	+	−0.043
E. croccoinguinis	86	+	+	−0.013
E. lacrimosus	11	−	−	0.660°
E. lanthanites	68	−	−	0.339°°
E. martiae	18	+	+	0.047
E. ockendeni	18	+	+	0.311
E. pseudoacuminatus	12	−	+	0.458
E. variabilis	148	−	+	0.128
I. quixensis	23	+	+	0.367
L. andreae	12	+	−	0.393
L. mystaceus	16	+	+	0.374
C. marchesianus	40	+	−	0.204
D. parvulus	109	+	+	0.119
D. pictus	48	+	+	0.305°
P. femoralis	12	+	+	0.509
H. albogutatata	21	+	+	0.322
H. bifurca	20	+	+	0.472°
H. boans	25	+	+	0.411°
H. bokermanni	29	+	+	0.146
H. brevifrons	15	+	+	0.526°
H. calcarata	10	+	+	0.311
H. cruentomma	18	+	−	−0.023
H. fasciata	27	+	+	0.316
H. funerea	13	+	+	0.474
H. garbei	21	−	+	−0.055
H. granosa	11	+	+	0.636°
H. lanciformis	23	+	+	−0.154
H. leucophyllata	12	+	+	0.032
H. marmorata	10	+	+	0.089
H. parviceps	101	+	+	0.466°°
H. punctata	15	+	+	0.367
H. rhodopepla	52	−	+	−0.025
H. rubra	66	+	+	0.278
H. savayacuensis	14	+	+	0.545°
H. triangulum	19	+	+	0.323
P. palliata	15	+	−	0.204
P. tarsius	15	+	+	0.083
B. typhonius	14	+	+	0.893°°
D. minutus	41	+	+	−0.198
R. palmipes	25	+	−	0.173

°°, $P<0.01$; °, $P<0.05$; +, normal distribution; −, non-normal distribution.

vegetation above water, and non-aquatic eggs with direct development. The variables (mean snout-vent length and mean number of mature ovarian eggs for each species) were transformed to their natural logarithms to reduce curvilinearity. In each case, after transformation the variables are normally distributed, and the correlation coefficient is significant ($0.05 > P > 0.01$) (Table 10). The regression of fecundity on size for the three modes is illustrated in figure 5. Within a reproductive mode, larger species produce more eggs.

The relationships of the remaining species are shown in figure 6. The variables were transformed to their natural logarithms; correlation and regression analyses were omitted due to small sample sizes. There is no apparent trend in the species that carry their larvae to water. Those species producing foam nests demonstrate a positive trend; larger species produce more eggs.

TEMPORAL VARIATION IN SNOUT-VENT LENGTH AND FECUNDITY

Six species (*Eleutherodactylus croceoinguinis, E. lanthanites, E. variabilis, Dendrobates parvulus, Hyla parviceps,* and *H. rubra*) were found in sufficient abundance throughout the year to permit an analysis of the variation of gravid female snout-vent length and fecundity. Five of the species are continuous breeders, and *H. rubra* is an opportunistic breeder. Only those months during which at least three gravid females of each species were found are included in the analysis of variance; sample size of individuals range from 3-33. In order to determine the relationships between snout-vent length, fecundity, and rainfall, each of the seven data sets for which the *F*-values are significant were plotted together with the monthly rainfall data (Figs. 7-11). Kendall's nonparametric rank correlation test was performed on the variables and in no case was there statistical significance.

Eleutherodactylus variabilis and *Hyla rubra* demonstrate significant between-

month variation in both snout-vent length and fecundity, although there is no significant correlation between the two variables (Table 11). For five of the seven months, fecundity of *H. rubra* seems to be related to snout-vent length, but in May there is a sudden decrease in fecundity. This may be related to the decrease in rainfall (Fig. 7), because the species is dependent upon ephemeral,

TABLE 10.—CORRELATION AND REGRESSION COEFFICIENTS OF SIZE-FECUNDITY DATA FOR THREE MODES OF REPRODUCTION.

Mode of Reproduction	No. Species	Correlation Coefficient (r)	Slope	Regression Coefficient
1	25	0.90194**	1.76776	— 0.20112
4	13	0.63867*	1.69396	— 1.16910
8	13	0.96874**	2.64399	— 6.14199

**, $P<0.01$; *, $P<0.05$.

TABLE 11.—ANALYSES OF VARIANCE OF TEMPORAL VARIATION IN FEMALE SNOUT-VENT LENGTH AND FECUNDITY.

		Mean Square	df	F-Ratio	Fisher's Exact P
E. croceoinguinis					
SVL	Between Months	2.74160	6	3.383	0.00545
	Within Months	0.81043	76		(0.01)
# Eggs	Between Months	1.99199	6	1.566	0.16815
	Within Months	1.27235	76		(NS)
E. lauthanites					
SVL	Between Months	7.13837	5	0.950	0.54285
	Within Months	7.51366	58		(NS)
# Eggs	Between Months	116.55457	5	3.323	0.01053
	Within Months	35.07288	58		(0.05)
E. variabilis					
SVL	Between Months	4.63847	11	4.271	0.00007
	Within Months	1.08606	134		(0.001)
# Eggs	Between Months	8.54161	11	3.054	0.00139
	Within Months	2.79688	134		(0.01)
H. parviceps					
SVL	Between Months	2.79295	8	1.764	0.09232
	Within Months	1.58350	103		(NS)
# Eggs	Between Months	19403.552	8	3.090	0.00394
	Within Months	6280.4565	103		(0.01)
H. rubra					
SVL	Between Months	6.57784	6	2.452	0.03488
	Within Months	2.68232	57		(0.05)
# Eggs*	Between Months	58872.717	6	2.988	0.01313
	Within Months	19700.828	57		(0.05)
D. parvulus					
SVL	Between Months	1.34580	10	1.840	0.06363
	Within Months	0.73145	94		(NS)
# Eggs	Between Months	2.79793	10	0.559	0.84367
	Within Months	5.00589	94		(NS)

* Variances heteroscedastic.

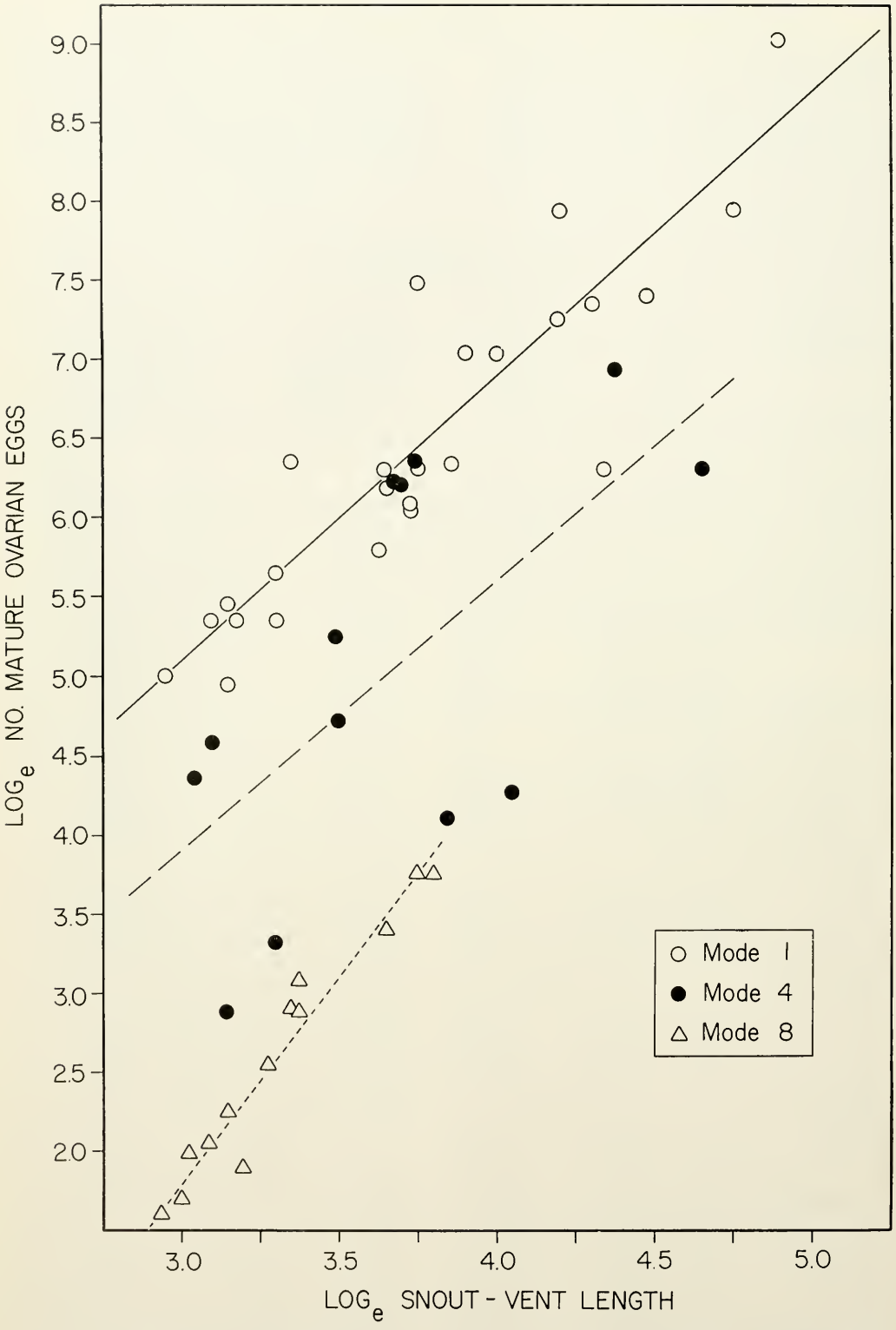

FIG. 5.—Size-fecundity relationships for three modes of reproduction. Mode 1 = eggs deposited in water, free-swimming aquatic larvae; mode 4 = eggs deposited on vegetation above water, free-swimming aquatic larvae; mode 8 = terrestrial or arboreal eggs, direct development. See table 10 for correlation and regression coefficients.

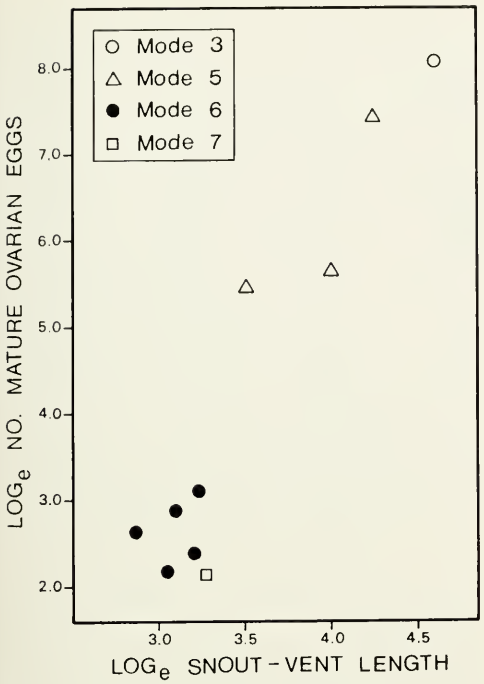

FIG. 6.—Size-fecundity relationships for four modes of reproduction. Mode 3 = eggs deposited in constructed basin, free-swimming aquatic larvae; mode 5 = eggs suspended in foam nest, free-swimming aquatic larvae; mode 6 = terrestrial eggs, larvae carried to water on dorsum of adult; mode 7 = eggs suspended in foam nest, larvae develop in foam.

water-filled ditches and ponds for breeding. There is a trend toward decreasing fecundity in *E. variabilis* from July through June, whereas fecundity in *H. rubra* seems to be cyclic. Because of the continued abundance of individuals and the fact that *E. variabilis* occurs in open areas, around human habitation, I assume that collecting did not disturb females enough to lower fecundity. There are several possible explanations for variation in snout-vent length, although no supporting evidence is available. It is conceivable that differential predation on large versus small females may have resulted in significantly different monthly means. Also, breeding cycles coupled with age at maturity may have resulted in variation in both snout-vent length and fecundity. Temporal variation in snout-vent length and fecundity is not significantly correlated with rainfall in either species (Figs. 7-8). The two smallest mean snout-vent lengths of *E. variabilis* are during the months following greatest rainfall; fecundity decreases slightly from the preceding month in both cases.

Eleutherodactylus croceoinguinis demonstrates significant monthly variation in snout-vent length, and both *E. lanthanites* and *Hyla parviceps* show significant between-month variation in fecundity. None of these variables is significantly correlated with rainfall. The fecundity relationships of the latter two species parallel those of *E. variabilis* and *H. rubra*. *Eleutherodactylus lanthanites* decreases in fecundity throughout the study period and *H. parviceps* shows cyclic variation in fecundity (Figs. 9-10). Although there is no significant

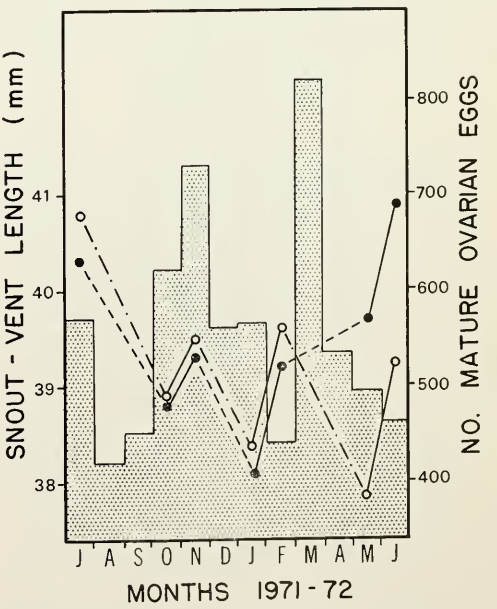

FIG. 7.—Relationships between snout-vent length, fecundity, and rainfall per month (note: the far left is July 1971, with June 1972 on the right) for *Hyla rubra*. For the rainfall scale see figure 9. The closed circles represent snout-vent length, the open circles, number of mature ovarian eggs. The solid lines connect consecutive months, dashed lines, non-consecutive months. Stippled area represents rainfall.

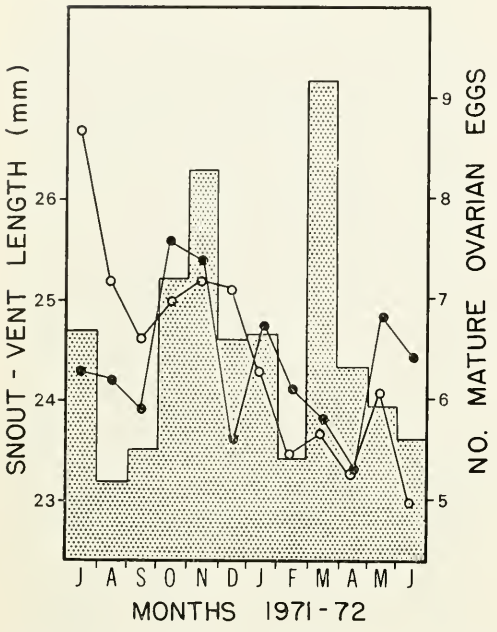

Fig. 8.—Relationships between snout-vent length, fecundity, and rainfall per month for *Eleutherodactylus variabilis*. For the rainfall scale see figure 9. The closed circles represent snout-vent length, the open circles, number of mature ovarian eggs.

correlation with monthly rainfall, fecundity of the latter species may be related to weekly rainfall. Because tree frogs of mode 1 are dependent upon water for egg deposition and subsequent larval development, they probably are capable of regulating egg production and maturation in close association with climatic variation. There are no obvious explanations for decreasing fecundity in *E. lanthanites* and the significant between-month variation in size of gravid *E. croceoinguinis* (Fig. 11); environmental variables regulating reproductive performance of species with direct development are extremely difficult to interpret. There is no significant monthly variation in either snout-vent length or fecundity in *Dendrobates parvulus*.

Volumetric Relationships

Body volume and volume of the mature ovarian complement were measured by water displacement for 23 species of frogs (Table 12). A product-moment correlation analysis was run on the 23 species as a group in order to determine the relationship between snout-vent length and body volume, using means for each species. The non-transformed data yield a significant correlation coefficient of 0.892 ($P < 0.01$). A second analysis was run on the ten species that deposit eggs in water; again the coefficient (0.916) is highly significant ($P < 0.01$). In both cases the relationship is curvilinear, supporting the commonly accepted theory that volume increases at a much greater rate than does body length. Because body volume is a more realistic measure of an animal's "size" than is snout-vent length, volume probably is a more accurate measure of size in the determination of size-fecundity relationships.

A third variable relevant to fecundity is body weight. Two studies have concluded that weight and snout-vent length

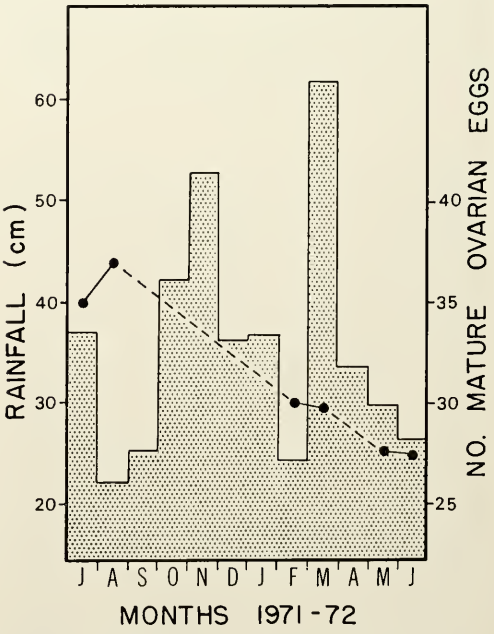

Fig. 9.—Relationship between rainfall and fecundity for *Eleutherodactylus lanthanites*. The solid lines connect consecutive months, the dashed lines, non-consecutive months.

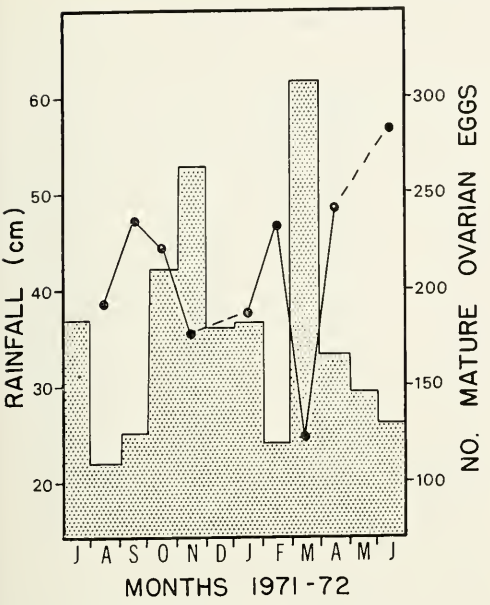

FIG. 10.—Relationship between rainfall and fecundity for *Hyla parviceps*. The solid lines connect consecutive months, the dashed lines, non-consecutive months.

are highly correlated in lizards (Davis, 1967; Turner and Gist, 1970). Gromko, Mason, and Smith-Gill (1973) examined the relationship between dry weight and volume of tadpoles. They found that the volume$^{1/3}$ of water displaced by a tadpole is highly correlated with dry weight at metamorphosis. This correlation is much greater than that for snout-vent length with dry weight, indicating that volume$^{1/3}$ is a more reliable indicator of biomass than weight. Whether a 1:1 relationship between weight and volume exists in frogs is unknown.

We can re-examine fecundity-size relationships among 23 species of frogs by using volume as the index of size. In order to minimize the spread of data points and reduce curvilinearity, the mean body volumes and egg volumes were transformed to their natural logarithms; the data are distributed normally. The points were plotted and the regression line computed (Fig. 12); the correlation coefficient (0.976) is highly significant ($P < 0.01$). Thus, species with larger body volumes have larger volumes of eggs. This relationship prevails within the reproductive modes studied. In the ten species that deposit eggs in water, the correlation coefficient (0.870) is significant ($P < 0.01$); positive trends are evident for the other modes.

Clutch volume expressed as a percentage of the total volume was examined (Table 12). The means for the 23 species range from 3.1 to 18.2 per cent, the smallest being that of the largest species, *Bufo marinus* (fecundity based on ovarian count = 6000 eggs) and the largest percentage being that of

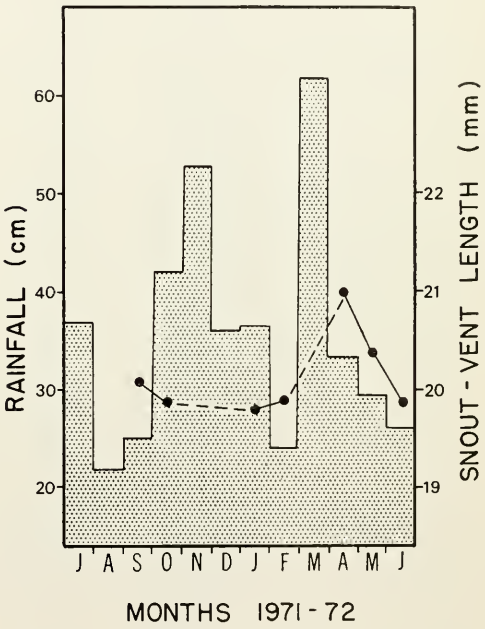

FIG. 11.—Relationship between rainfall and snout-vent length for *Eleutherodactylus croceoinguinis*. The solid lines connect consecutive months, the dashed lines, non-consecutive months.

the small tree frog *Hyla cruentomma* (mean fecundity = 472.9 eggs). The product-moment correlation coefficient between snout-vent length and per cent clutch volume is -0.376 ($P < 0.1$). The inverse relationship indicates that as snout-vent length increases, proportionately less of the total volume is accounted

TABLE 12.—SUMMARY OF VOLUMETRIC DATA FOR 23 SPECIES BASED ON MATURE OVARIAN EGG COMPLEMENT.[1]

Species	N	♀ SVL	Vol. ♀	Vol. Eggs	Vol. Eggs / Vol. Female	No. Eggs	Diam. Eggs
E. croceoinguinis	8	21.0-22.5 (21.5)	0.6-0.9 (0.7)	<0.05-0.05 (<0.05)	<6.3-8.3 (<7.2)	5-9 (6.4)	2.0-3.0 (2.4)
E. lanthanites	7	38.0-41.0 (39.8)	3.0-4.0 (3.6)	0.2-0.4 (0.3)	5.0-11.4 (7.5)	22-37 (30.3)	2.0-3.0 (2.6)
E. ockendeni	3	29.0-30.0 (29.3)	1.5-1.7 (1.6)	0.1 (0.1)	5.9-6.7 (6.3)	14-15 (14.3)	2.5-3.0 (2.7)
E. variabilis	20	24.0-28.0 (25.3)	0.8-1.1 (0.9)	0.05-0.1 (0.08)	5.0-11.1 (8.1)	5-11 (7.9)	2.0-3.0 (2.5)
I. quixensis	2	54.0-55.0 (54.5)	13.0 (13.0)	0.8-1.0 (0.9)	6.2-7.7 (7.0)	31-33 (32.0)	4.0 (4.0)
L. andreae	5	26.5-30.0 (28.2)	1.3-2.0 (1.7)	0.1-0.2 (0.1)	5.3-11.8 (8.4)	7-11 (8.6)	2.0-3.0 (2.5)
L. wagneri	1	77.0	38.0	3.3	8.7	3150	1.0
C. marchesianus	10	18.0-19.0 (18.5)	0.5-0.6 (0.5)	<0.05-0.5 (<0.05)	<8.3-10.0 (<9.3)	11-20 (16.5)	1.5 (1.5)
D. parvulus	5	21.5-23.0 (22.1)	0.7-0.9 (0.8)	0.05-0.1 (0.08)	6.2-11.1 (9.6)	9-12 (10.0)	2.0-3.0 (2.4)
D. pictus	10	22.0-26.0 (24.0)	0.8-1.4 (1.0)	0.1-0.2 (0.1)	8.3-14.3 (10.8)	16-37 (21.6)	2.0 (2.0)
H. bokermanni	5	24.0-28.5 (25.7)	0.9-1.1 (1.0)	0.1 (0.1)	9.1-11.1 (10.5)	80-130 (103.2)	1.0 (1.0)
H. cruentomma	7	25.0-29.5 (27.6)	0.9-1.4 (1.2)	0.1-0.3 (0.2)	11.1-25.0 (18.2)	300-580 (472.9)	1.0 (1.0)
H. garbei	8	42.0-47.0 (44.6)	4.0-5.3 (4.3)	0.3-1.0 (0.6)	8.6-20.0 (14.4)	460-930 (686.3)	1.0 (1.0)
H. lanciformis	13	87.0-91.0 (89.1)	35.0-40.0 (37.2)	2.5-6.5 (5.3)	6.8-17.6 (14.3)	1400-3300 (2252.3)	1.5-2.0 (1.9)
H. parviceps	6	24.0-27.5 (25.8)	0.9-1.2 (1.1)	0.1-0.2 (0.1)	8.3-22.2 (11.2)	210-330 (249.2)	1.0 (1.0)
H. punctata	15	35.0-41.0 (37.8)	2.5-3.5 (2.9)	0.2-0.5 (0.3)	6.7-16.7 (11.9)	270-440 (344.3)	1.0-1.5 (1.2)
H. rhodopepla	14	25.5-30.5 (27.9)	1.2-1.7 (1.4)	0.1-0.5 (0.2)	8.3-29.4 (14.6)	210-720 (363.6)	1.0 (1.0)
H. rubra	17	38.0-43.0 (40.3)	3.0-4.7 (3.7)	0.3-1.0 (0.6)	9.4-22.5 (16.8)	440-780 (642.6)	1.0-1.5 (1.2)
H. triangulum	11	36.0-41.5 (40.0)	3.0-4.5 (3.9)	0.2-0.6 (0.4)	5.0-15.0 (9.4)	320-520 (462.3)	1.0-1.5 (1.2)
P. palliata	1	46.5	5.5	0.5	9.1	55	2.6
B. marinus	1	140.0	240.0	7.5	3.1	6000	1.1
B. typhonius	2	65.0-68.0 (66.5)	20.0 (20.0)	1.3-1.5 (1.4)	6.5-7.5 (7.0)	540-1350 (945.0)	1.5 (1.5)
R. palmipes	4	107.0-118.5 (113.9)	90.0-132.0 (119.3)	4.5-10.0 (7.4)	4.4-7.6 (6.1)	2400-3900 (3025.0)	1.5-2.0 (1.8)

[1] For each species, numbers on the top line represent ranges; numbers in parentheses below are means.

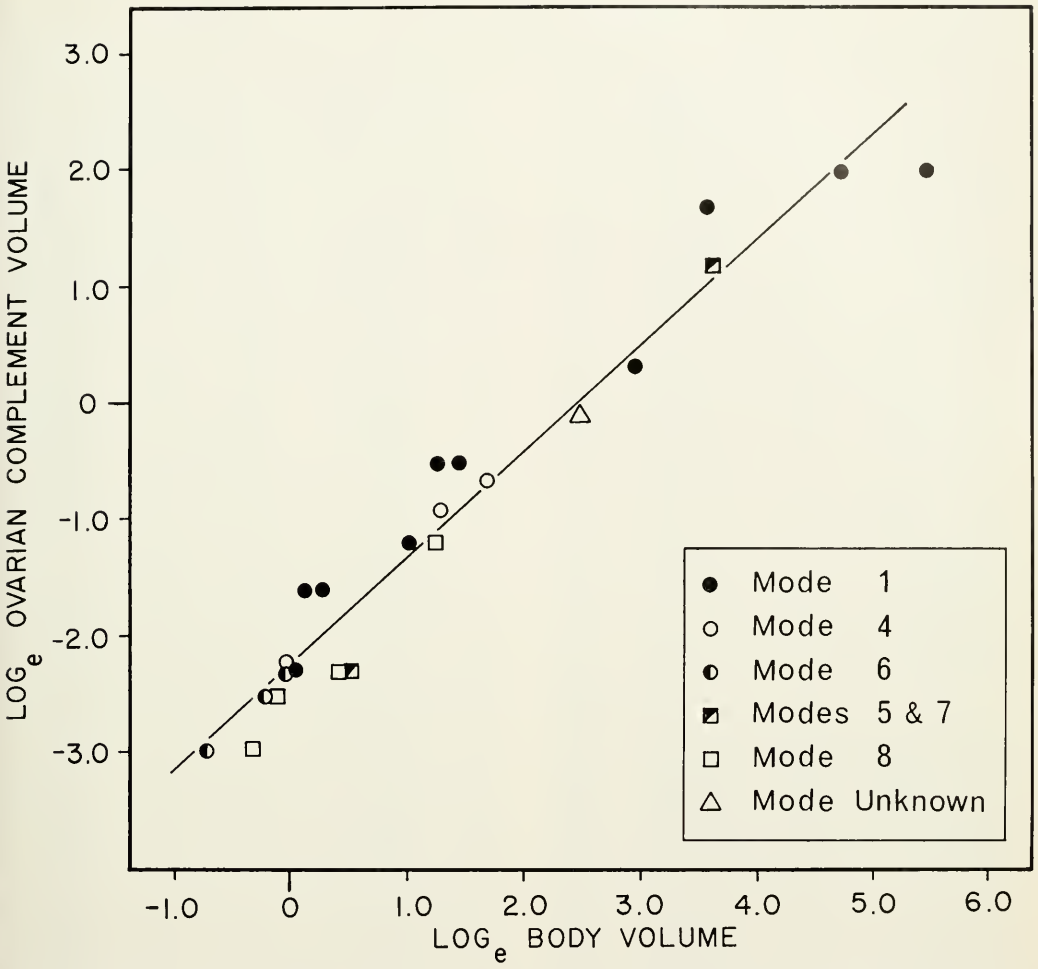

FIG. 12.—Relationship between mean body volume of gravid females and mean volume of mature ovarian complements for 23 species. Mode 1 = eggs deposited in water; mode 4 = eggs deposited on vegetation above water; mode 6 = terrestrial eggs, larvae carried to water on dorsum of adult; mode 5 = eggs suspended in foam nest, free-swimming aquatic larvae; mode 7 = eggs suspended in foam nest, larvae develop in foam; mode 8 = terrestrial or arboreal eggs, direct development.

for by the egg mass. This is probably so because large species have a proportionately larger amount of supportive tissue.

Sexual Dimorphism in Size

Male and female snout-vent lengths (ranges, means, and sex ratios) for 61 species of frogs representing seven reproductive modes are summarized in table 13. Homoscedasticity of variances was tested (F_{max} test); in every case, there is no significant difference in variance between males and females within a species. Student's t-tests indicate that in all species except two, females are significantly larger than males ($0.05 > P > 0.001$). There is no significant difference between sexes in *Hyla boans* and *Hyla punctata* ($P < 0.4$ and 0.9, respectively). Males of the former species are slightly larger than females.

Species size probably is determined to some extent by interspecific size relations (as studied by Schoener, 1970), but this does not account for the signifi-

TABLE 13.—SEXUAL DIMORPHISM IN SIZE FOR GRAVID FEMALES AND ADULT MALES OF 61 SPECIES OF ANURANS.

Species	Males			Females			Ratio	
	N	Range SVL	$\bar{X}$	N	Range SVL	$\bar{X}$	♀ SVL / ♂ SVL	t
H. alboguttata	10	27.0-31.0	28.8	10	35.0-45.0	40.7	1.41	10.980***
H. calcarata	10	32.0-38.0	35.9	10	47.0-61.0	53.9	1.50	13.769***
H. cruentomma	10	24.0-28.0	26.2	10	26.0-30.0	27.6	1.05	2.278*
H. fasciata	10	33.0-37.0	35.7	10	45.0-50.0	47.7	1.34	17.955***
H. fuscra	10	31.0-36.0	33.2	10	33.0-43.0	38.0	1.14	4.474***
H. garbei	10	34.0-38.0	35.4	10	41.0-45.0	42.0	1.19	10.378***
H. geographica	10	40.0-49.0	44.2	7	64.5-68.0	66.6	1.51	16.744***
H. granosa	10	36.0-43.0	39.0	10	40.0-44.0	41.2	1.06	2.713*
H. lanciformis	10	71.0-80.0	74.9	10	81.5-94.0	87.0	1.16	7.204***
H. marmorata	10	35.0-43.0	39.1	10	46.0-53.0	49.3	1.26	10.465***
H. minuta	4	20.0-22.0	21.3	5	23.0-24.0	23.8	1.12	5.338**
H. parviceps	10	16.0-18.0	17.1	10	20.5-25.0	23.1	1.35	13.306***
H. punctata	10	33.0-40.0	36.4	10	35.0-40.0	36.8	1.01	0.432ns
H. rhodopepla	10	18.0-23.0	21.3	10	27.0-27.5	27.2	1.28	11.184***
H. rubra	10	31.0-34.0	32.3	10	35.0-41.0	38.7	1.20	9.185***
H. boliviana	10	32.0-37.0	34.3	2	40.0-44.0	42.0	1.22	-----
R. palmipes	10	88.0-102.0	92.3	10	108.0-125.0	116.8	1.27	9.219***
B. marinus	10	87.0-127.0	104.1	5	115.0-146.0	132.6	1.27	4.350***
B. typhonius	10	41.0-62.0	52.3	10	58.0-86.0	75.3	1.44	6.156***
D. minutus	10	13.0-15.0	14.2	10	18.0-21.0	19.4	1.37	12.333***
H. boans	10	81.0-116.0	103.8	10	80.0-110.0	98.0	0.94	1.258ns
H. bifurca	10	23.0-26.0	25.1	10	29.0-34.0	31.8	1.27	12.712***
H. bokermanni	10	20.0-23.0	22.0	10	23.0-25.5	23.9	1.09	4.749***
H. brevifrons	10	16.0-20.0	18.3	10	18.0-23.0	21.0	1.15	3.793**
H. leucophyllata	10	32.0-36.0	33.9	10	40.0-44.0	42.0	1.24	12.320***
H. sarayacuensis	10	23.0-27.0	25.0	10	31.0-37.0	33.5	1.34	11.920***
H. triangulum	10	23.0-28.0	25.5	10	36.0-39.0	37.6	1.47	21.909***
P. palliata	10	40.0-44.0	42.1	10	44.0-49.0	46.3	1.10	5.579***
P. tarsius	10	83.0-92.0	86.9	10	100.0-111.0	104.9	1.21	10.320***
P. tomopterna	10	42.0-47.0	45.3	5	55.0-60.0	57.2	1.26	13.260***
P. vaillanti	10	49.0-56.0	52.1	5	68.0-84.0	78.8	1.51	12.211***
L. discodactylus	7	26.0-29.0	27.4	5	33.0-35.0	33.6	1.23	10.089***
L. mystaceus	10	49.0-53.0	51.3	10	53.0-58.0	55.0	1.07	5.543***
L. wagneri	10	42.0-59.0	48.4	6	51.0-80.0	68.2	1.41	4.745***
L. andreae	10	22.0-26.0	24.3	10	25.0-29.0	26.5	1.09	4.208***
C. marchesianus	10	16.0-17.0	16.4	10	16.0-18.0	17.0	1.04	2.250*
C. sauli	4	20.0-22.0	21.3	4	24.0-26.0	24.8	1.16	5.170**
D. parvulus	10	18.0-20.0	18.6	10	20.0-22.0	21.1	1.13	7.777***
D. pictus	10	18.0-21.0	19.5	10	20.0-24.0	22.1	1.13	5.332***
P. femoralis	10	21.0-25.0	23.4	10	24.0-28.0	25.9	1.11	3.883**
E. acuminatus	8	17.0-21.0	18.9	5	27.0-31.0	29.2	1.54	11.027***
E. altamazonicus	10	17.0-21.0	18.6	10	27.0-31.0	28.5	1.53	16.896***
E. conspicillatus	10	26.0-30.0	28.5	10	40.0-44.0	42.2	1.48	22.940***
E. croceoinguinis	10	14.0-16.0	15.1	10	20.0-22.0	20.4	1.35	14.957***
E. lacrimosus	10	17.0-23.0	19.5	10	22.0-29.0	24.2	1.24	5.850***
E. lanthanites	10	25.0-29.0	26.8	10	36.0-42.0	39.0	1.46	14.077***
E. martiae	10	14.0-17.0	15.3	10	19.0-23.0	21.7	1.42	13.509***
E. ockendeni	10	17.0-21.0	18.8	10	24.0-28.0	26.3	1.40	12.257***
E. pseudo-acuminatus	10	16.0-19.0	16.9	10	19.0-22.0	21.0	1.24	9.460***
E. variabilis	10	16.0-18.0	16.7	10	23.0-26.0	24.3	1.46	20.642***
I. quixensis	10	39.0-48.0	42.2	10	48.0-56.0	52.7	1.23	8.310***

***, $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns, not significant.

cant sexual dimorphism in size characteristic of nearly all of the species examined. There are at least two possible explanations for the dimorphism. Firstly, although the sizes of males are limited by certain physiological and functional restrictions, it probably is advantageous for individuals to be as small as possible, in order to reduce energy expenditure for body maintenance; furthermore, a small male is less apt to compete with a larger female for available food resources. Secondly, larger females can accommodate either larger eggs or more eggs. If reproductive efficiency requires increased energy expenditure to increment the egg mass, there will be a selective advantage for increased female body size. However, there is an upper limit beyond which it is neither efficient nor feasible to grow due to the physiological stresses and energetics involved in the production of additional eggs. There is also an opposing selective force operant on females, which, like males, must restrict body size as much as possible to conserve energy for body maintenance.

Due to the allometric relationship between surface and volume one would expect that large frogs could carry a much greater volume of eggs relative to their body length than small frogs. However, my results show that small species have a greater proportion of the total body volume represented by eggs than do larger species. Thus, the total length of an animal is perhaps a greater limit to fecundity for smaller species than for larger ones.

If size (measured by either snout-vent length or body volume) is "critically" important in fecundity of small species, the following prediction can be made: sexual dimorphism in size should be greater in small species than in large species, within a reproductive mode. Given the correlation between size and fecundity within a reproductive mode, a second prediction follows: within any reproductive mode, sexual dimorphism in size should be positively correlated with fecundity. The results of Kendall rank-order correlation tests on species within each of the four reproductive modes represented by at least five species indicate that there is no correlation between either female snout-vent length or body volume and sexual dimorphism in size. Neither is there any correlation between fecundity and size dimorphism. But, in general, those species with the most similar sexual dimorphism in size are members of the same species group. For example, the pairs *Hyla granosa* and *H. punctata,* and *Hyla calcarata* and *H. geographica,* and the trio *Hyla bifurca, H. sarayacuensis,* and *H. triangulum* are all the most similar species in sexual dimorphism in size, each pair or trio belonging to the same species group. Both predictions are rejected, and it is concluded that sexual dimorphism in size is determined more by systematic relationships than by reproductive considerations.

Mean snout-vent length ratios of amplectant pairs of frogs found in the field were calculated and compared with those figures obtained from random samples of gravid females and adult males (Table 14). Statistical tests were not run on the data due to small sample sizes in most cases. Of the 20 species, 14 show 0.05 units or less variation between the two ratios. The ratios of amplectant *Bufo marinus* and *Hyla lanciformis* indicate less sexual dimorphism in size than the random samples indicate, whereas there is greater sexual dimorphism in size in *Hyla bifurca, H. bokermanni, H. marmorata,* and *H. parviceps* than expected by the random sample ratios. Males were larger than anticipated in the two large species and smaller than expected in the tree frogs less than 50.0 mm mean snout-vent length.

Assortative mating is related to sexual size dimorphism. Data on snout-vent lengths and female-to-male ratios for 96 pairs of frogs of 20 species found amplexing in the field are summarized in table 14. Product-moment correlations were

Table 14.—Comparison of Female-to-Male Snout-Vent Length Ratios of Amplectant Pairs Found in the Field Versus Ratios Calculated from Random Samples.[1]

Species	N	Mean ♂ SVL	Mean ♀ SVL	♀ SVL / ♂ SVL	Random Sample Ratio
E. acuminatus	1	19.5	31.0	1.59	1.54
E. altamazonicus	9	19.1	28.4	1.50	1.53
E. croceoinguinis	9	15.1	20.2	1.34	1.35
E. lacrimosus	2	20.3	24.8	1.22	1.24
E. lanthanites	1	25.5	38.5	1.51	1.46
E. martiae	8	15.3	21.8	1.43	1.42
E. ockendeni	2	19.5	26.5	1.36	1.40
E. paululus	1	15.0	19.0	1.27	-----
E. pseudoacuminatus	3	17.3	20.5	1.19	1.24
E. variabilis	10	16.4	23.6	1.45	1.46
B. marinus	3	111.0	124.0	1.12	1.27
H. bifurca	1	23.5	33.5	1.43	1.27
H. bokermanni	2	21.0	24.8	1.18	1.09
H. brevifrons	6	18.3	20.6	1.13	1.15
H. cruentomma	4	25.3	26.3	1.04	1.05
H. garbei	19	34.7	41.7	1.20	1.19
H. lanciformis	1	81.0	84.5	1.04	1.16
H. marmorata	6	37.3	49.6	1.33	1.26
H. parviceps	5	16.4	24.4	1.49	1.35
P. palliata	1	44.0	48.0	1.09	1.10

[1] See Table 13 for results of *t*-tests for each species and sample sizes for the random samples.

run on the four species with sample sizes of nine or greater (*Hyla garbei, Eleutherodactylus altamazonicus, E. croceoinguinis*, and *E. variabilis*) in order to determine if large females "choose" large males. The null hypothesis, that there is no significant correlation between snout-vent lengths, was accepted on the basis of the correlation coefficients (-0.014, -0.068, 0.083, and 0.092, respectively). Thus, there is no apparent assortative mating regarding size in these four species.

Developmental Relationships

In order to study developmental relationships between fecundity, ovum diameter, number of days until hatching, size at hatching, and ovarian size factor, I brought amplectant and ovulated frogs into the laboratory, where they deposited eggs. Egg deposition and hatching were successful for 18 species (Table 15). All containers of developing eggs were kept in the shade in one corner of the laboratory in order to approximate identical developmental conditions for all species. Because intraoval developmental time is probably temperature-dependent, it is likely that shade had a negative influence on duration of development.

Ten species of hylids are represented by sufficient data to warrant statistical analysis of the variables (Table 16). There is no significant correlation between snout-vent length and fecundity in any of the species.

The measurement of egg diameter is not sufficiently accurate (only to the nearest 0.5 mm) to allow rigorous analysis of its relation to other developmental variables, but in certain instances trends are suggested. Only four of the above species (*Hyla bokermanni, H. marmorata, H. triangulum*, and *Phyllomedusa tarsius*) vary in egg diameter. Larger individuals of the first two species deposit smaller eggs ($r = -0.933$, $P < 0.01$ and $r = -0.596$, $P < 0.01$, respectively), although there is no evidence of greater fecundity. For *P. tarsius*, the more eggs produced, the smaller they are ($r = -0.932$, $P < 0.05$). Within

mode 1 (eggs deposited in water), species with the largest clutch sizes also have the largest ova diameters, probably due to overall body size. This trend is not evident for those species of mode 4 (eggs deposited on vegetation above water), possibly because the range of clutch sizes is much narrower than in mode 1.

Salthe and Duellman (1973) concluded that, regardless of reproductive mode, the larger the ovum diameter, the

TABLE 15.—SUMMARY OF DEVELOPMENTAL DATA FOR 18 SPECIES OF FROGS[1]

Species	N	Female SVL	No. Eggs	Diam. Eggs	Devel. Time	Size Hatchling	Ovarian Size Factor
E. martiae	1	22.0	8	3.5	26.0 (N=1)	5.0 (N=1)	1.27
E. pseudoacuminatus	1	19.5	7	3.5	30.0 (N=2)	5.0 (N=2)	1.26
H. bifurca	15	30.0-35.0 (33.3)	153-255 (191.0)	2.0 (2.0)	5.0-5.6 (5.2)	6.0-7.0 (6.5)	11.47
H. bokermanni	20	24.5-28.5 (26.8)	86-196 (127.2)	1.5-2.0 (1.6)	4.0-5.3 (4.3)	4.0-4.5 (4.2)	7.59
H. brevifrons	1	21.0	73	1.5	6.3	6.0	4.52
H. calcarata	3	52.5-57.0 (55.0)	1060-1250 (1153.3)	2.0 (2.0)	3.3-3.6 (3.4)	5.5-7.0 (6.0)	41.94
H. cruentomma	5	25.0-28.0 (27.2)	590-1200 (884.0)	1.5 (1.5)	1.6 (1.6)	3.5-4.0 (3.8)	48.75
H. garbei	18	37.0-45.0 (41.3)	445-905 (727.1)	1.5 (1.5)	2.3-3.3 (2.9)	4.5-5.5 (5.0)	26.41
H. lanciformis	3	(87.3)	2100-2400 (2250.0)	2.0 (2.0)	3.3 (3.3)	6.0 (6.0)	51.55
H. leucophyllata	3	43.0-44.0 (43.3)	570-769 (669.7)	1.5 (1.5)	3.6-4.0 (3.7)	5.0-6.0 (5.3)	23.20
H. marmorata	6	48.0-53.0 (49.8)	740-1580 (1170.3)	1.5-2.0 (1.7)	1.3-2.0 (1.6)	5.0-5.5 (5.1)	39.95
H. parviceps	13	23.5-26.0 (24.9)	242-520 (311.3)	1.0 (1.0)	1.3-2.3 (1.9)	4.0-4.5 (4.1)	12.50
H. punctata	1	36.0	310	1.5	3.6	4.0	12.92
H. rhodopepla	43	26.0-29.5 (28.1)	253-526 (353.4)	1.0 (1.0)	2.3-3.3 (2.9)	5.0-5.5 (5.0)	12.58
H. rubra	3	40.0-42.0 (40.8)	745-807 (777.3)	1.5 (1.5)	2.0-2.3 (2.1)	4.5-5.0 (4.7)	28.58
H. sarayacuensis	7	35.0-39.0 (36.4)	92-138 (113.1)	2.0 (2.0)	5.3-18.3 *	7.0-9.0 *	6.21
H. triangulum	9	35.0-42.5 (38.1)	465-690 (550.9)	1.5-2.0 (1.6)	3.0-4.6 (3.8)	5.0-6.0 (5.4)	23.13
P. tarsius	5	95.0-110.0 (104.3)	426-640 (536.2)	3.5-4.0 (3.7)	7.0-8.3 (7.4)	11.5-13.0 (12.6)	19.02

* Dependent upon site of development (in or out of water).

[1] Except for the three *H. lanciformis*, eggs were deposited and hatched in the laboratory; the ovarian size factor for this species is based on the mean SVL from Table 8.

TABLE 16.—PRODUCT-MOMENT CORRELATION COEFFICIENTS OF REPRODUCTIVE DATA FROM INDIVIDUALS DEPOSITING EGGS IN THE LABORATORY, FAMILY HYLIDAE.[1]

Species	N	Correlation Coefficient			Normality		
		SVL/*N* eggs	SVL/ egg. diam.	*N* eggs/ egg diam.	SVL	*N* eggs	egg diam.
H. cruentomma	5	0.618 (NS)	X	X	+	+	X
H. garbei	18	0.432 (NS)	X	X	+	+	X
H. marmorata	6	0.028 (NS)	−0.933 (.01)	−0.256 (NS)	+	+	+
H. parviceps	13	0.179 (NS)	X	X	+	+	X
H. rhodopepla	43	0.034 (NS)	X	X	−	+	X
H. bifurca	15	0.140 (NS)	X	X	+	+	X
H. bokermanni	20	−0.301 (NS)	−0.596 (.01)	−0.179 (NS)	+	+	−
H. sarayacuensis	7	0.627 (NS)	X	X	+	+	X
H. triangulum	9	−0.310 (NS)	−0.413 (NS)	0.611 (NS)	+	+	−
P. tarsius	5	0.579 (NS)	−0.396 (NS)	−0.932 (.05)	−	+	+

[1] An X indicates that correlation was not computed because of the absence of variation in egg diameter for the particular species. A "+" indicates that the data are distributed normally, and a "−" indicates a significant departure from normality.

larger the hatchling. They also stated that a negative correlation exists between ovum size and intraoval developmental time. Although there is much overlap in mean ovum diameter between the two hylid modes of reproduction 1 and 4, there is no overlap in the intraoval developmental time (Fig. 13).

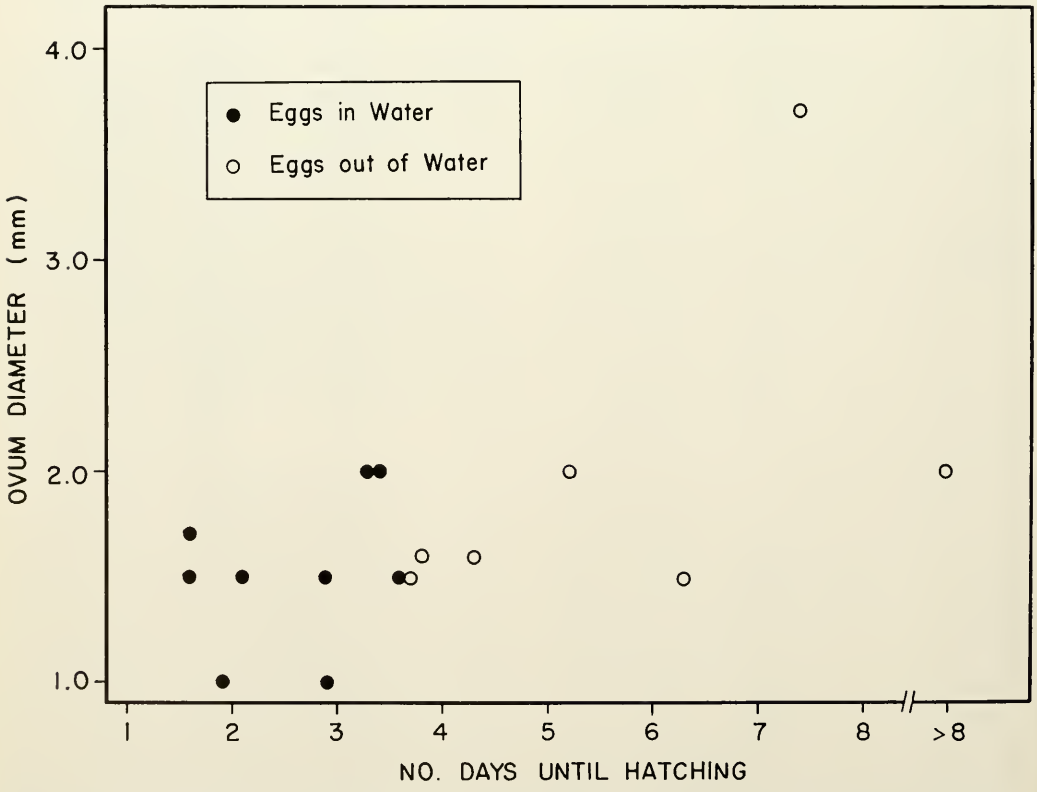

FIG. 13.—Relationship between intraoval developmental time and ovum diameter for 16 species of tree frogs of two modes of reproduction.

Without exception, all species depositing eggs on vegetation above water take longer to develop and hatch than those depositing eggs in water. There is no apparent relationship between ovum diameter and intraoval developmental time within the species of mode 1; the range of variation of both variables is slight (Fig. 13). With the exception of two species (*Hyla brevifrons* and *H. sarayacuensis*), representatives of mode 4 indicate a positive relationship between ovum diameter and number of days until hatching. Hatchling size ranges from 3.8 to 6.0 mm for species of mode 1 and from 4.2 to 12.6 mm for species of mode 4.

Developmental time (and therefore hatchling size) in mode 4 is probably more the result of a synergistic interaction of factors than the sole result of ovum diameter. There is less temperature fluctuation affecting aquatic eggs than those deposited on vegetation, and the effects of wind and rain are probably greater on mode 4 than on mode 1 eggs. Experimentation in the laboratory indicates that for egg clutches of *Phyllomedusa* and *Hyla* (both *leucophyllata* and *parviceps* groups), hatching time is reduced and often initiated by the occasional sprinkling of water onto the clutch. *Hyla bifurca* eggs took equal amounts of time to develop and hatch whether placed in shallow water or entirely out of water, whereas eggs of *H. sarayacuensis* developed nearly twice as rapidly when placed in shallow water as when left out of water.

On 29 April 1973, a gravid female and male of each of four species of the *Hyla leucophyllata* group were collected; subsequently they deposited eggs in the laboratory. The four sets of eggs were raised under identical environmental conditions. There are two reproductive patterns in this species group. The two smallest species, *H. bifurca* and *H. sarayacuensis*, have the lowest fecundity and the largest ovum diameter; the eggs take longer to hatch than the other two species, and the resultant larvae are larger (Table 17). At the end of ten days the tadpoles maintain a size advantage over the larvae of *H. leucophyllata* and *H. triangulum*. Because most of the species breed sympatrically and synchronously, the intraoval developmental time and hatchling size differences may represent an evolutionary step towards possible reduction of larval competition.

TABLE 17.—COMPARISONS OF DEVELOPMENTAL DATA FOR FOUR SPECIES OF THE *Hyla leucophyllata* GROUP.

	H. bifurca	*H. leucophyllata*	*H. sarayacuensis*	*H. triangulum*
SVL Female (mm)	32.5	43.0	36.0	40.0
No. Eggs	173	570	138	546
Ovum Diam. (mm)	2.0	1.5	2.0	1.5
# Days 'til Hatch.	5.0	3.6	5.3–6.0	3.6
Size Hatchling (mm)	6.5	6.0	7.0	5.5
Size 2 Days	8.0	7.0	8.5	6.5
Size 4 Days	9.0	8.0	9.0	7.0
Size 6 Days	9.0	8.0	10.0	7.5
Size 8 Days	9.5	8.5	10.5	8.0
Size 10 Days	9.5	8.5	10.5	8.0

RELATION OF REPRODUCTIVE VARIABLES TO AQUATIC SITE

A fundamental consideration in size-fecundity relationships is whether a frog can invest less energy into body maintenance (small body size) and reproduction (lower fecundity) if the egg deposition site is less vulnerable to predators. It can be predicted that within the genus *Hyla*, species that deposit eggs in open, unprotected bodies of water (mode 1) have a greater egg mass, including both fecundity and ovum diameter, relative to body length (ovarian size factor) than species that deposit eggs on vegetation above water (mode 4). Fifteen species of *Hyla* of mode 1

and seven species of mode 4 (data from Table 8) indicate that species that deposit eggs in water have a significantly higher egg mass relative to body size (snout-vent length) than do those species that deposit eggs out of water ($t = 2.222$, $P < 0.05$). The range of the former mode is 8.89 to 42.00 ($\bar{X} = 20.47$), and the latter is 3.78 to 20.94 ($\bar{X} = 11.08$).

As previously indicated, the species of *Hyla* that deposit eggs in water require fewer days to hatch than those species depositing eggs on vegetation above water. This is presumed to increase chances of survival in a temporary aquatic environment. The longer the tadpoles take to hatch, the greater the risk of their environment drying up before metamorphosis is completed. Also, the more rapid is development, the less vulnerable are the eggs to aquatic predators; once the tadpoles hatch, they are capable of actively avoiding predators.

It can be predicted that within species of *Hyla* (mode 1 only), those breeding in ephemeral and temporary water should have a greater egg mass relative to snout-vent length (ovarian size factor) than those species breeding in more permanent environments. The following species were examined—ephemeral to more temporary environment: *H. garbei, H. lanciformis, H. marmorata,* and *H. rubra;* less temporary to permanent environment: *H. calcarata, H. cruentomma, H. funerea, H. geographica, H. granosa, H. parviceps, H. punctata,* and *H. rhodopepla.* The ovarian size factors for the first group range from 19.72 to 37.06 ($\bar{X} = 26.60$) and for the second group from 10.05 to 42.00 ($\bar{X} = 19.73$). A Student's *t*-test indicates a non-significant difference between the two groups ($t = 1.057$, $P < 0.4$), although the mean is larger for the first group, as predicted. The fact that fecundity is not greater in those species breeding in more temporary environments suggests that either temporary environments are not a greater risk in terms of survivorship or some other mechanism is compensating for the hazards of the unpredictability. Perhaps there is less predator pressure in temporary water and/or species in temporary water undergo development and metamorphose faster than their counterparts in more permanent environments and therefore are subjected to aquatic predators for a shorter period of time. No supporting data for these suggestions are available at present.

Intraoval developmental time and size of hatchling for temporary versus permanent environments for species within mode 1 (same groups as in preceding test) were examined (data from Table 15). The range in developmental time for the first group is 1.6 to 3.3 days ($\bar{X} = 2.48$) and 1.6 to 3.6 ($\bar{X} = 2.68$) for the second. The range in hatchling size is 4.7 to 6.0 mm ($\bar{X} = 5.20$) and 3.8 to 6.0 mm ($\bar{X} = 4.58$) for the first and second groups, respectively. Student's *t*-tests indicate no significant differences; values of *t* are 0.363 ($P < 0.9$) for developmental time and 1.178 ($P < 0.4$) for hatchling size.

Comparison of Fecundity Measures

Mature ovarian complement size was compared to the number of eggs deposited for 26 species (Table 18). Females were dissected after oviposition in the laboratory to learn if the entire clutch had been deposited; in each case, all or nearly all the eggs were released. Therefore, the two fecundity measures are comparable. Four of the 16 species tested by Student's *t*-tests show significant differences ($P < 0.05$) between the two measures. All are tree frogs having a mean fecundity of greater than 500 eggs (*Hyla cruentomma, H. garbei, H. rubra,* and *H. triangulum*). In each case a significantly greater number of eggs was deposited in the laboratory than indicated by the mean ovarian egg count. The discrepancy may be due to small sample sizes of deposited eggs, especially for *H. cruentomma* and *H. rubra.*

TABLE 18.—COMPARISON OF MATURE OVARIAN EGG COMPLEMENT AND ACTUAL NUMBER OF EGGS DEPOSITED FOR 26 SPECIES.

Species	Ovarian Complement				Deposited Eggs					
	N	Range *N* eggs	Mean *N* eggs	Max. Diam.	*N*	Range *N* eggs	Mean *N* eggs	Range Diam.	Mean Diam.	[a] *t*
E. altamazonicus	20	12-25	18.2	2.5	3	17-20	18.7	3.0	3.0	—
E. croceoinguinis	86	2-7	4.8	3.0	2	4-6	5.0	3.5	3.5	—
E. lacrimosus	11	7-16	9.5	2.5	1	7	7.0	4.5	4.5	—
E. lanthanites	68	20-52	30.4	3.0	1	30	30.0	4.0	4.0	—
E. martiae	18	5-13	7.8	2.0	4	8-10	8.8	3.0-3.5	3.3	0.554ns
E. pseudoacuminatus	12	4-11	7.3	3.0	1	7	7.0	3.5	3.5	—
E. variabilis	148	2-11	6.7	3.0	6	5-11	7.2	4.0	4.0	1.240ns
H. bifurca	8	163-210	186.0	1.5	15	153-255	191.0	2.0	2.0	0.165ns
H. bokermanni	29	65-135	98.3	1.5	20	86-196	127.2	1.5-2.0	1.6	0.367ns
H. brevifrons	15	48-114	79.1	1.0	6	48-91	70.0	1.0-1.5	1.3	0.683ns
H. calcarata	10	835-1600	1143.5	1.5	3	1060-1250	1153.3	2.0	2.0	—
H. cruentomma	18	280-1200	580.4	1.0	5	590-1200	884.0	1.5	1.5	3.170**
H. garbei	21	280-793	550.8	1.5	18	445-905	727.1	1.5	1.5	4.057***
H. geographica	7	1780-4300	2797.1	1.0	1	2434	2434.0	2.0	2.0	—
H. lanciformis	23	740-2400	1617.5	2.0	1	2310	2310.0	2.0	2.0	—
H. leucophyllata	6	420-910	587.8	1.5	4	570-928	797.5	1.5	1.5	1.946ns
H. marmorata	7	630-1260	979.4	1.5	6	740-1580	1170.3	1.5-2.0	1.7	1.361ns
H. parviceps	101	120-395	234.1	1.0	13	242-520	311.3	1.0	1.0	2.052ns
H. punctata	20	230-430	324.6	1.5	2	310-420	365.0	1.5	1.5	—
H. rhodopepla	52	140-422	285.4	1.0	43	253-526	353.4	1.0	1.0	1.886ns
H. rubra	66	315-960	591.4	1.5	4	620-807	738.0	1.5	1.5	2.522*
H. sarayacuensis	14	68-176	113.4	2.0	14	85-138	105.1	2.0	2.0	0.335ns
H. triangulum	23	320-650	501.7	1.5	10	465-690	557.8	1.5-2.0	1.6	2.365*
P. palliata	15	38-106	60.8	2.5	6	38-71	49.3	3.5-4.0	3.6	0.920ns
P. tarsius	15	410-750	548.7	3.0	8	426-650	551.0	3.5-4.0	3.7	0.030ns
P. vaillanti	5	912-1250	1114.4	2.0	1	645	645.0	2.0	2.0	—

[a] Student *t*-tests were computed on sample sizes of a random 10 individuals wherever possible; where sample size is less than 10, the entire sample was used. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

SYNTHESIS OF RESULTS BY REPRODUCTIVE MODE

The 30 species that deposit eggs in water (mode 1) demonstrate a wide range in each of the reproductive variables. Included in this mode are the smallest (19.1 mm snout-vent length) to the next-to-the-largest species (132.6 mm) at Santa Cecilia. Fecundity ranges from 143 eggs for *Sphaenorhychus carneus* to more than 8500 eggs for *Bufo marinus*. On an overall basis, larger species produce more eggs ($P < 0.01$). However, only three of the 16 species tested show a significant correlation between snout-vent length and fecundity. The range in maximal ovarian egg diameter is 1.0 to 2.0 mm, which together with snout-vent length and fecundity yields a wide range in the ovarian size factor index (6.22 to 97.26). The larger the body volume, the greater the egg complement volume. Sexual dimorphism in snout-vent length ranges from essentially none (female-to-male ratio of *Hyla punctata* = 1.01) to the female being half again the size of the male (ratio = 1.51 for *Hyla geographica*). Species with the largest clutch sizes also have the largest ovum diameters. There is no apparent relationship between ovum diameter and intraoval developmental time, although this may be due to only slight range in variation of both variables. There is no significant relationship between either developmental time or hatchling size and the "permanence" of the environment. All of the species have at least slightly pigmented eggs. Some species breed in ephemeral and/or temporary water, others in permanent water. Fecundity is not significantly greater ($P < 0.4$) in those species breeding in ephemeral–temporary water than for those breeding in more permanent water. Some species breed in the forest, others in forest-edge environments, and others in disturbed, open areas; the breeding habitat is unknown for many of the species. Species breed continually, opportunistically, or sporadically.

Nyctimantis rugiceps is the only representative of mode 2 reproduction. No gravid females were found. Males call continually throughout the year from water-filled tree cavities (often bamboo trees) in both forest and forest-edge environments. It is assumed that eggs are deposited in the cavities and that larval development occurs therein.

Mode 3 reproduction is represented only by the large tree frog, *Hyla boans* (mean female snout-vent length = 99.0 mm). The mean number of ovarian eggs is 3154.8, and the maximum ovarian egg diameter is 2.0 mm, yielding an extremely high ovarian size factor of 63.73. Larger females (snout-vent length) produce significantly more eggs ($P < 0.05$). Males are slightly larger than females. Eggs are heavily pigmented. The only breeding site of *H. boans* is along the edge of the river. Breeding is sporadic, usually during drier periods when the river level is low.

Thirteen species deposit eggs on vegetation above water (mode 4). These range in size from small tree frogs (20.9 mm snout-vent length, *Hyla brevifrons*) to the large *Phyllomedusa tarsius* (105.3 mm). Likewise, fecundity exhibits a wide range, from 18 eggs of *Centrolenella munozorum* to over 1000 eggs for *Phyllomedusa vaillanti*. On an overall basis, larger species produce more eggs ($P < 0.05$). Only three of the eight species tested for size-fecundity correlations show a significant relationship ($P < 0.05$). Maximal ovarian egg diameter ranges from 1.0 to 3.5 mm, yielding a wide spectrum of ovarian size factors (1.17 to 28.28). There is a trend for species with larger body volumes to have larger ovarian egg complement volumes. The female-to-male snout-vent length ratios range from 1.09 for *Hyla bokermanni* to 1.51 for *Phyllomedusa vaillanti*. Tadpoles of species of mode 4 take longer to hatch than those of species that deposit eggs directly in water. With the exception of two species, there is a positive relationship between ovum diameter and number of days until hatch-

ing. The sprinkling of water onto the egg clutch speeds up the developmental process and initiates hatching in some species. Species of this reproductive mode have a significantly lower egg mass relative to body length than those species that deposit eggs in water. Egg pigmentation ranges from none to heavy. Species breed over still and running water, in ephemeral, temporary, and permanent situations. Breeding occurs in forest, forest-edge, and disturbed, open areas. None of the species breeds continually; of those known, all are opportunistic or sporadic breeders.

Five leptodactylids produce foam nests and have aquatic larval development (mode 5); quantitative reproductive data are available for three of these. Snout-vent length ranges from 33.6 mm (*Leptodactylus discodactylus*) to 68.2 mm (*Leptodactylus wagneri*), and fecundity from 234.8 eggs to 1740.0 eggs for the same two species, respectively. Maximal ovarian egg diameter ranges from 1.0 mm for *L. discodactylus* to 2.5 mm for *L. mystaceus*. The ovarian size factors range from 6.99 to 38.27. Sexual dimorphism in size ranges from practically none (female-to-male snout-vent length ratio = 1.07, *L. mystaceus*) to 1.41, *L. wagneri*. *Leptodactylus wagneri* is the only one of these three species with egg pigmentation. Breeding habitats are known for three species: *L. mystaceus* and *L. wagneri* breed in open, disturbed areas and in forest-edge environments, and *L. pentadactylus* breeds in forest and forest-edge situations. *Leptodactylus mystaceus* is considered to be a continuous breeder, and *L. pentadactylus* a drier-period, sporadic breeder.

Five dendrobatids deposit terrestrial eggs and the larvae subsequently are carried to water on the dorsum of the adult (mode 6). All are small frogs (snout-vent lengths from 17.8 to 25.6 mm) and have low fecundity (8.9 to 22.7 eggs). *Dendrobates pictus* is the only species having a significant ($P < 0.05$) correlation between snout-vent length and fecundity. Maximal ovarian egg diameter ranges from 1.5 to 3.0 mm; the ovarian size factors all are extremely low (0.66 to 1.77). Volumetric data were taken for three species; as expected, the species with the greatest snout-vent length (*Dendrobates pictus*) has the greatest body volume and egg complement volume. There is little variation in sexual dimorphism in snout-vent length (female-to-male ratios range from 1.04 to 1.16). Eggs are moderately pigmented in all species. All species breed in forest and/or forest-edge environments based on calling activity of the males and occurrence of gravid females. Based on the occurrence of gravid individuals and juveniles, it is suggested that all species except *Colostethus sauli* (for which there are few data) are continuous breeders.

Leptodactylus andreae is the only species that produces a foam nest in which the larvae undergo complete development (mode 7). The mean snout-vent length of gravid females is 26.7 mm, and the mean number of mature ovarian eggs is 8.7. There is no significant correlation between snout-vent length and fecundity. The maximal ovum diameter is 3.0 mm; the ovarian size factor is low (0.98). Females are significantly ($P < 0.001$) larger than males, although the female-to-male snout-vent length ratio is low (1.09). The eggs are unpigmented. Gravid females were found sporadically throughout the year in forest and forest-edge environments.

Fourteen species of *Eleutherodactylus* deposit terrestrial or arboreal eggs which undergo direct development (mode 8). Most species are small, ranging in snout-vent length from 19.0 to 44.5 mm. Fecundity is low (4.8 to 43.0 eggs) and ovarian egg diameter is large (2.0 to 3.5 mm). The ovarian size factors are correspondingly low, ranging from 0.66 for *E. paululus* to 3.54 for *E. conspicillatus*. Generally, larger species produce more eggs ($P < 0.01$). Three of the nine species tested show significant correlation ($P < 0.05$ to 0.01) be-

tween snout-vent length and fecundity. Volumetric data are available for four species. The larger the mean snout-vent length of the species, the larger is the mean body volume and egg complement volume. Females are significantly larger than males ($P < 0.001$) in each of the ten species examined; the female-to-male ratios are large, ranging from 1.24 to 1.54. Developmental data are available for only two species. An *E. martiae* deposited eight eggs (mean diameter = 3.5 mm); one egg hatched 26 days later; hatchling size was 5.0 mm. An *E. pseudoacuminatus* deposited seven eggs (mean diameter = 3.5 mm); two eggs hatched 30 days later; each hatchling was 5.0 mm snout-vent length. Eggs of all species are unpigmented. Some species breed in the forest, others at the forest-edge, and others in disturbed, open areas; breeding sites of several species are unknown. Gravid females of three species are found throughout the year, and are presumably continual breeders. Gravid females of seven species are found sporadically.

Hemiphractus proboscideus is the only terrestrial species which presumably provides complete parental care for young which undergo direct development (mode 10). No gravid females were found. Because all individuals (adults and young) were found in mature or second-growth forest, it is assumed that breeding occurs there. No information is available on breeding frequency.

The mode of reproduction is unknown for three leptodactylids (*Edalorhina perezi, Ischnocnema quixensis,* and *Lithodytes lineatus*). These species range in snout-vent length from 38.0 mm (*E. perezi*) to 52.9 mm (*I. quixensis*), and number of mature ovarian eggs ranges from 35.1 (*I. quixensis*) to 195.0 (*L. lineatus*). The low fecundity of *I. quixensis* suggests that development might be direct. On the other hand, the size of the ovarian complement of *L. lineatus* suggests the possibility of egg suspension in a foam nest. Size-fecundity relationship was examined for *I. quixensis;* there is no significant correlation. The maximal ovarian egg diameter is 4.0 mm for *I. quixensis* and 2.0 mm for the other two species; the ovarian size factors range from 2.65 to 7.65. Female *I. quixensis* are 1.23 times as large as males. Eggs are unpigmented in all three species. The breeding habitats of the species are unknown; gravid *I. quixensis* were found throughout the year, suggesting that the species is a continuous breeder.

The greatest amount of variation in the reproductive characters examined occurs among the species that deposit eggs in bodies of water other than tree holes or constructed nests. This may be due to the fact that this is the largest group (30 of the 74 species). Or, it may be the result of a wider spectrum of morphological and physiological possibilities (related to the energetics of reproduction) available to the species. The least amount of variation is found among the five species that carry their larvae to water. The character states of eight reproductive variables for each of the 74 species are summarized in coded form in table 20 (see Table 19 for translation of code). The following outline indicates the relationship of the species within each reproductive mode:

I. Eggs Deposited in Water; Tadpoles Develop in Water
  A. Eggs Deposited in Ditches, Puddles, Swamps, Ponds, Lake, and Streams (32 species)
    1. Large body size (SVL > 60 mm)
      a. Less than 600 eggs
        (1) *Osteocephalus taurinus*
      b. 1000 to 3000 eggs
        (1) *Bufo typhonius*
        (2) *Hyla geographica*
        (3) *Hyla lanciformis*
        (4) *Phrynohyas coriacea*
        (5) *Rana palmipes*
      c. More than 8000 eggs
        (1) *Bufo marinus*
      d. Fecundity unknown
        (1) *Bufo glaberrimus*
    2. Medium body size (SVL = 30 to 60 mm)
      a. Less than 500 eggs
        (1) *Hyla alboguttata*

(2) *Hyla granosa*
(3) *Hyla punctata*

b. 500 to 800 eggs
(1) *Hyla fasciata*
(2) *Hyla funerea*
(3) *Hyla garbei*
(4) *Hyla rubra*
(5) *Osteocephalus buckleyi*

c. More than 800 eggs
(1) *Hyla calcarata*
(2) *Hyla marmorata*
(3) *Osteocephalus lepreurii*
(4) *Hamtophryne boliviana*

3. Small body size (SVL < 30 mm)

a. Less than 175 eggs
(1) *Dendrophryniscus minutus*
(2) *Sphaenorhynchus carneus*

b. 200 to 300 eggs
(1) *Hyla minuta*
(2) *Hyla parviceps*
(3) *Hyla rhodopepla*
(4) *Chiasmocleis bassleri*
(5) *Chiasmocleis anatipes*
(6) *Chiasmocleis ventrimaculata*

c. More than 500 eggs
(1) *Hyla cruentomma*

d. Fecundity unknown
(1) *Hyla riveroi*

B. Tree Cavity
1. *Nyctimantis rugiceps*

C. Constructed Basin
1. *Hyla boans*

II. Eggs Deposited out of Water; Tadpoles Develop in Water (23 species)

A. Eggs Deposited on Vegetation Above Water

1. Less than 30 eggs
a. *Centrolenella midas*
b. *Centrolenella munozorum*

2. More than 60 eggs

a. Eggs unpigmented; usually > 2.0 mm diameter

(1) Small egg mass relative to body length (ovarian size factor < 5.0)
(a) *Phyllomedusa palliata*
(b) *Phyllomedusa tomopterna*

(2) Large egg mass relative to body length (ovarian size factor > 15.0)
(a) *Phyllomedusa tarsius*
(b) *Phyllomedusa vaillanti*

b. Eggs slightly to heavily pigmented; usually < 2.0 mm diameter

(1) Small body size (SVL < 25 mm); less than 100 eggs
(a) *Hyla bokermanni*
(b) *Hyla brevifrons*

TABLE 19.—CODE OF REPRODUCTIVE STRATEGY CHARACTERS.

I.	Mean Female Snout-Vent Length	
	1) ≤ 30.9 mm	4) 61.0-75.9 mm
	2) 31.0-45.9 mm	5) 76.0-90.9 mm
	3) 46.0-60.9 mm	6) ≥ 91 mm
II.	Mean Number Mature Ovarian Eggs	
	1) 1.0-10.9	11) 301.0-400.9
	2) 11.0-20.9	12) 401.0-500.9
	3) 21.0-30.9	13) 501.0-600.9
	4) 31.0-50.9	14) 601.0-700.9
	5) 51.0-75.9	15) 701.0-800.9
	6) 76.0-100.9	16) 801.0-1000.9
	7) 101.0-150.9	17) 1001.0-2000.9
	8) 151.0-200.9	18) 2001.0-3000.9
	9) 201.0-250.9	19) 3001.0-5000.9
	10) 251.0-300.9	20) ≥ 5001
III.	Maximum Ovarian Egg Diameter	
	1) ≤ 1.0 mm	5) 2.6-3.0 mm
	2) 1.1-1.5 mm	6) 3.1-3.5 mm
	3) 1.6-2.0 mm	7) ≥ 3.6 mm
	4) 2.1-2.5 mm	
IV.	Ovarian Size Factor	
	1) 0.01-5.00	7) 30.01-35.00
	2) 5.01-10.00	8) 35.01-40.00
	3) 10.01-15.00	9) 40.01-45.00
	4) 15.01-20.00	10) 45.01-50.00
	5) 20.01-25.00	11) ≥ 50.01
	6) 25.01-30.00	
V.	Sexual Size Dimorphism (♀/♂ SVL)	
	1) 0.91-1.00	5) 1.31-1.40
	2) 1.01-1.10	6) 1.41-1.50
	3) 1.11-1.20	7) 1.51-1.60
	4) 1.21-1.30	
VI.	Breeding Habitat ("Non-aquatic" includes constructed basin + tree hole)	
	1) Aquatic—forest	
	2) Aquatic—forest edge	
	3) Aquatic—disturbed area	
	4) 1 & 2	
	5) 1 & 3	
	6) 2 & 3	
	7) 1, 2, & 3	
	8) Aquatic—unknown	
	9) Non-aquatic—forest	
	10) Non-aquatic—forest edge	
	11) Non-aquatic—disturbed area	
	12) 9 & 10	
	13) 9 & 11	
	14) 10 & 11	
	15) 9, 10, & 11	
	16) Non-aquatic—unknown	
	17) Unknown	
VII.	Frequency of Breeding	
	1) Continuous	3) Sporadic
	2) Opportunistic	4) Unknown
VIII.	Egg Pigmentation	
	1) Unpigmented	
	2) Slightly pigmented	
	3) Moderately to heavily pigmented	
	4) Unknown	

TABLE 20.—CHARACTER STATES OF EIGHT REPRODUCTIVE CHARACTERS FOR 74 SPECIES OF FROGS, BY REPRODUCTIVE MODE.

See Table 19 for translation of character states. An asterisk indicates data from Lago Agrio (16 km. from Santa Cecilia).

Species	$\bar{X}$ ♀ SVL	$\bar{X}$ N Eggs	Maximum Egg Diameter	Ovarian Size Factor	Sexual Size Dimorphism	Breeding Habitat	Breeding Frequency	Egg Pigmentation
MODE 1								
B. glaberrimus	--	--	--	--	--	8	4	4
B. marinus	6	20	2	11	4	3	3	3
B. typhonius	4	17	3	9	6	4	1	3
D. minutus	1	7	1	2	5	8	1	3
H. alboguttata	2	12	2	4	6	8	3	3
H. calcarata	3	17	2	7	6	4	3	3
H. cruentomma	1	13	1	5	2	4	3	3
H. fasciata	3	13	2	4	5	8	1	3
H. funerea	2	13	1	3	3	4	3	3
H. garbei	2	13	2	4	3	7	1	3
H. geographica	4	18	1	9	7	1	3	3
H. granosa	2	12	2	4	2	1	3	3
H. lanciformis	5	17	3	8	3	6	1	3
H. marmorata	3	16	2	6	4	7	2	3
H. minuta	1	9	1	2	3	8	4	3
H. parviceps	1	9	1	3	5	4	1	3
H. punctata	2	11	2	3	2	7	3	3
H. rhodopepla	1	10	1	3	4	7	2	3
H. riveroi	--	--	--	--	--	8	4	4
H. rubra	2	13	2	4	3	6	2	3
*O. buckleyi**	3	13	1	3	--	8	4	3
*O. leprieurii**	3	16	1	3	--	8	3	3
O. taurinus	5	13	1	2	--	8	4	3
P. coriacea	4	17	3	9	--	8	4	3
S. carneus	1	7	1	2	--	1	4	2
C. anatipes	--	--	--	--	--	1	4	--
C. bassleri	1	9	1	2	--	8	4	3
C. ventrimaculata	1	9	1	2	--	8	4	3
H. boliviana	2	17	1	9	4	4	3	3
R. palmipes	6	18	3	10	4	7	1	3
MODE 2								
N. rugiceps	--	--	--	--	--	12	4	4
MODE 3								
H. boans	6	19	3	11	1	10	3	3
MODE 4								
C. midas	1	3	2	1	--	8	4	2
C. munozorum	1	2	2	1	--	1	4	1
H. bifurca	2	8	2	2	4	6	2	3
H. bokermanni	1	6	2	2	2	7	2	2
H. brevifrons	1	6	1	1	3	2	2	2
H. favosa	2	12	1	3	--	4	4	3
H. leucophyllata	2	13	2	5	4	4	3	2
H. sarayacuensis	2	7	3	2	5	7	2	2
H. triangulum	2	13	2	4	6	7	2	3
P. palliata	3	5	4	1	2	4	3	1
P. tarsius	6	13	5	4	4	4	3	1
P. tomopterna	3	5	6	1	4	4	3	1
P. vaillanti	5	17	3	6	7	1	3	1
MODE 5								
L. discodactylus	2	9	1	2	4	8	4	1

TABLE 20.—CHARACTER STATES OF EIGHT REPRODUCTIVE CHARACTERS FOR 74 SPECIES OF FROGS, BY REPRODUCTIVE MODE.—*Continued.*

See Table 19 for translation of character states. An asterisk indicates data from Lago Agrio (16 km. from Santa Cecilia).

Species	$\bar{X}$ ♀ SVL	$\bar{X}$ N Eggs	Maximum Egg Diameter	Ovarian Size Factor	Sexual Size Dimorphism	Breeding Habitat	Frequency Breeding	Egg Pigmentation
L. mystaceus	3	10	4	3	2	6	1	1
L. pentadactylus	--	--	--	--	--	4	3	3
L. wagneri	4	17	2	8	6	6	4	3
P. petersi	--	--	--	--	--	8	4	1
MODE 6								
C. marchesianus	1	2	2	1	2	12	1	3
C. sauli	1	2	2	1	3	9	4	3
D. parvulus	1	1	5	1	3	12	1	3
D. pictus	1	2	3	1	3	12	1	3
P. femoralis	1	3	3	1	3	12	1	3
MODE 7								
L. andreae	1	1	5	1	2	12	3	1
MODE 8								
E. acuminatus	1	2	4	1	7	9	3	1
E. altamazonicus	1	2	4	1	7	9	3	1
E. conspicillatus	2	4	6	1	6	9	3	1
E. croceoinguinis	1	1	5	1	5	9	1	1
E. diadematus	2	4	4	1	--	16	4	1
E. lacrimosus	1	1	4	1	4	9	3	1
E. lanthanites	2	3	5	1	6	12	1	1
E. martiae	1	1	3	1	6	12	3	1
E. ockendeni	1	2	5	1	5	9	3	1
E. paululus	1	1	4	1	--	16	4	1
E. pseudoacuminatus	1	1	5	1	4	10	3	1
E. quaquaversus	1	3	4	1	--	16	4	1
E. sulcatus	--	--	--	--	--	16	4	1
E. variabilis	1	1	5	1	6	14	1	1
MODE 10								
H. proboscideus	--	--	--	--	--	9	4	1
MODE UNKNOWN								
E. perezi	2	6	3	1	--	17	4	1
I. quixensis	3	4	7	1	4	17	1	1
*L. lineatus**	3	8	3	2	--	17	4	1

(2) Medium body size (SVL > 30 mm); more than 100 eggs
(a) Less than 200 eggs
(1) *Hyla bifurca*
(2) *Hyla sarayacuensis*
(b) More than 450 eggs
(1) *Hyla favosa*
(2) *Hyla leucophyllata*
(3) *Hyla triangulum*

B. Eggs Suspended in Foam Nest
1. Large body size (SVL > 60 mm); eggs moderately pigmented; males with prepollical spine
a. *Leptodactylus pentadactylus*
b. *Leptodactylus wagneri*
2. Small to medium body size (SVL < 60 mm); eggs unpigmented; males lacking prepollical spine
a. Foam nest produced on surface of water
(1) *Leptodactylus discodactylus*
(2) *Physalaemus petersi*
b. Foam nest produced in burrow
(1) *Leptodactylus mystaceus*

C. Terrestrial Eggs; Larvae Carried to Water on Dorsum of Adult
1. Fewer than 10 eggs
a. *Dendrobates parvulus*

2. 11 to 20 eggs
   a. Smaller egg mass relative to body length (ovarian size factor < 1.20)
      (1) *Colostethus marchesianus*
      (2) *Colostethus sauli*
   b. Larger egg mass relative to body length (ovarian size factor 1.60)
      (1) *Dendrobates pictus*
3. More than 20 eggs
   a. *Phyllobates femoralis*

III. Eggs and Young Completely Independent of Standing Water (16 species)
   A. Tadpoles Develop Within Foam Nest
      1. *Leptodactylus andreae*
   B. Direct Development
      1. No, or limited parental care
         a. Larger body size (SVL $>$ 35 mm); more than 25 eggs
            (1) *Eleutherodactylus conspicillatus*
            (2) *Eleutherodactylus diadematus*
            (3) *Eleutherodactylus lanthanites*
         b. Smaller body size (SVL $<$ 35 mm); less than 25 eggs
            (1) Less than 10 eggs
               (a) *Eleutherodactylus croceoinguinis*
               (b) *Eleutherodactylus lacrimosus*
               (c) *Eleutherodactylus martiae*
               (d) *Eleutherodactylus paululus*
               (e) *Eleutherodactylus pseudoacuminatus*
               (f) *Eleutherodactylus variabilis*
            (2) More than 10 eggs
               (a) *Eleutherodactylus acuminatus*
               (b) *Eleutherodactylus altamazonicus*
               (c) *Eleutherodactylus ockendeni*
               (d) *Eleutherodactylus quaquaversus*
         c. Size and fecundity unknown
            (1) *Eleutherodactylus sulcatus*
      2. Complete parental care
         a. *Hemiphractus proboscideus*

DISCUSSION

Among the 81 species of frogs known to occur at Santa Cecilia, ten modes of reproduction are represented, and many reproductive strategies are operant. The key aspects involved in reproductive strategies are (1) size of female, (2) ovarian complement and clutch size, (3) diameter of eggs, (4) egg deposition site, (5) type of development, and (6) frequency of breeding. Presumably, each species possesses an optimal set of reproductive characters for maintenance of its population. Some species produce many eggs relative to their body size, others few. Some produce large eggs, others small. Some species breed continually, others sporadically. Cole (1954), in discussing variations in life history patterns, considered the following as axiomatic, ". . . that the reproductive potentials of existing species are related to their requirements for survival; that any life history features affecting reproductive potential are subject to natural selection; and that such features observed in existing species should be considered as adaptations, just as purely morphological or behavioral patterns are commonly so considered." Keeping these assumptions in mind, we can ask, why does the great diversity in anuran species and their reproductive modes exist at Santa Cecilia?

Historical Zoogeography.—Vuilleumier (1971) suggested that the present biotic patterns in South America have been determined by paleoecological changes during the Pleistocene. The evidence is based on analyses of speciation patterns of the flora and fauna throughout the continent and on paleobotanical and geological studies that document climatic events. Many areas of disjunction, hybridization, secondary sympatry, and introgression seem to exist in the Amazon Basin. Haffer (1969) proposed that climatic oscillations during the Pleistocene resulted in alternating series of contractions and expansions of the rainforest in lowland tropical South America. He postulated that during dry phases the forest covered only small, disjunct areas; these isolated regions would have acted as refugia for forest animals. Local selection pressures would have resulted in differentiation among the populations of species inhabiting differ-

ent forest refugia. During the wetter phases, the forests expanded; where previously isolated populations came together, they formed the present complex patterns typical of zones of secondary contact. One of the nine forest refugia postulated by Haffer is the Napo region, in which Santa Cecilia is located. Vanzolini and Williams (1970) also concluded that the Napo region was a forest refugium from a study of morphological variation of *Anolis chrysolepis* from the Amazon Basin. In certain areas, large blocks of characters are correlated with one another and vary geographically in the same direction; these areas were termed "core areas," and were thought to be those regions in which populations had evolved as a unit. One of the four core areas is the lower eastern slopes of the Andes, including the area of Santa Cecilia. Similar patterns of speciation in the upper Amazon Basin were hypothesized for the *Leptodactylus marmoratus* group (Heyer, 1973) and for the *Hyla parviceps* group (Duellman and Crump, 1974).

If Santa Cecilia were indeed part of a forest refugium during the Pleistocene, the high species richness in great part may be explained on that basis. There was probably strong selection favoring the evolution of reproductive diversity to cope with the changing environment. Selective factors operant at the species level would encourage those modes of reproduction best adapted to the environment.

The specific geographical location of Santa Cecilia probably serves as another contributing factor to the high species richness. The site is peripheral to both the Amazon Basin and the eastern slopes of the Andes. Certain species are widespread Amazonian species; others occur only in the upper Amazon Basin, and others principally inhabit lower Andean slopes. Possibly many of the species at Santa Cecilia are living at or near their ecological limits; this may explain why many of the species are seemingly rare.

Aquatic Larvae Versus Direct Development.—About 20 per cent of the total species of frogs at Santa Cecilia are independent of open bodies of water in that the young undergo direct development. Orton (1949) pointed out that direct development occurs in 10 of the 13 families of frogs then considered valid. She noted the occurrence of direct development in the Pipidae, Microhylidae, Ascaphidae, Pelobatidae, Leptodactylidae, Bufonidae, Atelopodidae, Dendrobatidae, Hylidae, and Ranidae. Orton stated that on one hand there is the tendency toward elimination of the tadpole stage (direct development), while in the opposite direction, there is the tendency toward greater complexity of the tadpole stage, represented by many species. She considered this paradox to be "an excellent example of the random nature of evolutionary trends."

Istock (1967) proposed that complex life cycles (defined as the condition "when the individuals of a species consistently pass through 2 or more ecologically distinct phases") are inherently unstable over evolutionary time. His proposal is based on the assumption that the evolutionary adaptations of the different phases are essentially independent, and that this independence is responsible for the fact that the ecological advantages of neither phase are fully realized. He suggested that through evolutionary time selective forces are generated that favor the reduction or loss of one of the phases. One example he cited is that of the loss of the larval stage in some frogs. However, Istock did not discuss the fact that there are no neotenic tadpoles. Wassersug (1974) attributed this phenomenon to the functional morphology of tadpoles.

Elimination of the aquatic larval stage offers several advantages: competition with other aquatic animals is avoided, vulnerability to aquatic predators is absent, and "unpredictability," in terms of the environment evaporating or becoming unfavorable, is eliminated.

On the other hand, there has been vast radiation in tadpole morphology,

and the majority of species of frogs have tadpoles. The maintenance of the larval stage may be considered the result either of presence or of absence of selective forces. Perhaps selection favored the continuing existence of tadpoles in some species. (See Wassersug, 1974, for a discussion concerning the adaptive advantages of the larval stage in anurans.) Or, perhaps selection favored direct development. In those environments with highly unstable paleoclimatic histories, the most successful strategy may have been the elimination of the larval stage. However, it may be that the hylids, bufonids, and ranids, among others that presently occur at Santa Cecilia, evolved during a more stable climatic regime—in environments with plentiful and open bodies of water, such that there was no advantage of becoming more terrestrial. The absence of these selective forces, then, may have resulted in the maintenance of the larval stage.

Size and Fecundity.—The widespread tendency of animal groups to evolve toward larger physical size is implied in Cope's writings (1887 and 1896). The most recent analysis of this phenomenon (now referred to as Cope's Rule) was presented by Stanley (1973), whose premise was that for every evolving population there would be some optimal body size for the niche it occupies. Whether evolution is towards size increase or decrease depends on whether the mean body size in the original population is smaller or larger than this optimum. The niche and/or optimal body size may change through time, leading to the evolution of a new body size. Numerous examples indicate that most populations approach optimal body size from smaller rather than from larger sizes. One exception is amphibians, which have evolved from "medium-sized" ancestors rather than "small." Stanley suggested that perhaps an important consideration is the fact that the origin of amphibians was associated with a new environmental medium. He suggested that large size initially may have been a necessity to provide a high surface-to-volume ratio, because of dehydration problems associated with cutaneous water loss. Stanley noted that many small species of animals are morphologically unspecialized, whereas nearly all relatively large species are structurally specialized; "major adaptive breakthroughs" occur at relatively small body sizes.

Lending support to Stanley's contention, Salthe and Duellman (1973) suggested that "small body size in frogs is a preadaptation for reproductive experimentation." Within the anuran fauna at Santa Cecilia, some of the most "specialized" modes of reproduction (modes 6-8) are represented by relatively small species. Most large species have a relatively generalized mode of reproduction.

A constraint to the evolution of new body size may be the sizes of sympatric species. Several studies have been carried out concerning the sizes of species in a community (Hutchinson, 1959; Schoener, 1965; 1970). These studies reveal that body size ratios (ratio of largest species to the next-largest species) show a regular progression of size among species within a community. The proposed explanation is that individual species may be dividing the size of the food items according to their own body sizes. There may be selection for the evolution of different sizes to avoid overlap in prey size. Thus, even though it may be advantageous for a species to increase its body size for reproductive purposes, it then may not compete as well for food. Caldwell (1973) found a similar regular progression of body size ratios in communities of tree frogs in Oaxaca, México. She suggested that competition for food was possibly an important factor influencing body size. C. Toft (personal communication) came to a similar conclusion from preliminary observations on forest-floor frogs (*Eleutherodactylus* and dendrobatids) in Perú.

Numerous studies on the relationship between female size and fecundity

in animals have been carried out. Rensch (1960) showed that large-sized species of different groups of cold-blooded vertebrates produce more eggs than small species of the same groups. Tinkle, Wilbur, and Tilley (1970) examined interspecific relationships between size and fecundity within single-brooded, multiple-brooded, oviparous, viviparous, early-maturing, late-maturing, temperate, and tropical groups of lizards. In all groups except late-maturing and tropical, larger species have significantly more eggs than smaller species. Salthe (1969) noted the interspecific relationship between snout-vent length and fecundity in salamanders is dependent upon the body length. Clutch size increases slowly with increasing size of small species, but increases at a greater rate with increasing size of larger species. Tilley (1968) showed that four of five sympatric species of *Desmognathus* have a positive correlation between snout-vent length and fecundity, both intraspecifically and interspecifically. Salthe and Duellman (1973) concluded that within a given reproductive mode there is a positive correlation between female snout-vent length and clutch size in frogs. My data on the frogs at Santa Cecilia support this contention; within a given reproductive mode, as female body length increases, fecundity increases interspecifically (Table 10 and Fig. 5).

Natural Selection.—The theory of "*r* and *K* selection" has received much attention recently. The terms (Cody, 1966; MacArthur and Wilson, 1967) refer to the two components of natural selection; *r* (intrinsic rate of natural increase) is the density-independent component and *K* (carrying capacity) is the density-dependent component. Pianka (1970) emphasized that no species is completely "*r*-selected" or completely "*K*-selected"; he suggested that selection should be thought of as a continuum, from *r* to *K*. The strategy at the *r*-end is productivity; mortality is often catastrophic and density-independent. Species at the *K*-end of the continuum capitalize on efficiency; the strategy is to increase efficiency of environmental resource utilization and to produce a few extremely fit offspring. In *K*-selection, mortality is usually density-dependent.

A combination of the following four components of *r* are useful in determining the relative position of a species on the *r*-*K* continuum: (1) fecundity, (2) longevity, (3) age at first reproduction, and (4) number of breeding times per lifetime. In addition, one needs to know death rates and whether mortality is mainly density-dependent or independent. The only parameter affecting *r* measured in my study at Santa Cecilia is fecundity. Because the spread of fecundity is so large (means from 4.8 to 8598 eggs) for the species of frogs, the measure is probably of considerable importance and is used here as a crude estimate of *r*.

Using fecundity as the measure of *r*, the fauna can be positioned along the continuum. Those species which deposit many small eggs in unprotected bodies of water are referred to the *r*-end. These include many of the species from mode 1. Next are the members of mode 1 with lower fecundity, followed by *Hyla boans* which constructs a nest. Intermediate groups, following the continuum to the right are: (1) mode 4 (*Centrolenella*, *Hyla*, and *Phyllomedusa*), (2) mode 5 (*Leptodactylus* and *Physalaemus*), (3) mode 6 (the dendrobatids), and (4) mode 7 (*Leptodactylus andreae*). The preceding species exhibit neither an extreme *r* nor *K* strategy. They allocate more energy into the search for appropriate oviposition sites than do the species which deposit eggs in open water. Much energy probably is spent in the production of foam nests and in the transportation of tadpoles to open water. The two *K*-strategist groups are the 14 species of *Eleutherodactylus*, which deposit few, large eggs out of water, and *Hemiphractus* which presumably provides complete parental care to the eggs and young. All 15 species have

direct development. (Fecundity in the latter species has not been measured at Santa Cecilia, but an individual from the nearby locality of Puerto Libre had 26 mature ovarian eggs.)

The next aspect considered is the relationship between fecundity, position on the *r-K* continuum, and the environment. Those species which deposit many eggs in open bodies of water (*r*-strategists) generally breed in unpredictable environments such as ephemeral or temporary puddles, ditches, and ponds in open, disturbed or forest-edge areas. Examples of these species are *Bufo marinus* and many *Hyla*. Probably one of the biggest mortality factors is evaporation of the aquatic habitat, obviously a density-independent factor. The frogs have no way of predicting whether the water will persist long enough for the eggs to hatch and the tadpoles to metamorphose. The strategy is to breed repeatedly throughout the year (these species are generally continuous or opportunistic breeders), and to deposit many eggs at a time. The *K*-strategists are generally found in second-growth or mature forest. They are completely independent of open bodies of water. The species do not form breeding congregations, but are more widely dispersed in the forest. The life-span of the oviposition and developmental sites are more predictable than those of *r*-strategists. For these reasons, catastrophic mortality is probably relatively uncommon, and overall mortality is more density-dependent.

There is no apparent relationship between population density and relative position on the *r-K* continuum. (Densities are merely estimates based on field observations and are not the result of quantitative sampling methods.) The most abundant species are located all along the continuum. These are tree frogs which congregate at temporary ditches and ponds (*e.g., Hyla bifurca, parviceps, rhodopepla, triangulum*), *Bufo typhonius* and *Dendrophryniscus minutus, Leptodactylus mystaceus,* two dendrobatids (*Colostethus marchesianus* and *Dendrobates parvulus*), and several species of *Eleutherodactylus* (*e.g., croceoinguinis, lanthanites,* and *variabilis*). Rare species are represented by most of the modes of reproduction, some more towards the *r*-end and some more towards the *K*-end of the continuum. The low population densities (if not the result of sampling bias), may be due to one or all of the following reasons: the species may be living at the border of their ecological tolerance; collecting pressure in past years perhaps depleted populations; some species may require a long time to reach sexual maturity; and, individuals may breed only once per year, or even less frequently.

Reproductive Effort.—As in other vertebrates, the energy commitment in terms of gametes is much greater for the female frog than for the male. Spermatozoa are produced cheaply. Males often call indiscriminately, whether or not conditions for breeding are adequate, much less optimal. For example, males were often found calling from dry swamps. It seems to be advantageous for males to be reproductively ready continuously. However, females produce gametes with larger amounts of stored energy. Because the energy commitment of females is so much greater, it is advantageous to be reproductively ready only at the most favorable times. There is no doubt stronger selection against error in the female; she must "predict" when conditions are favorable and respond to the male accordingly.

There is much variation in the timing of ovulation and actual egg deposition among species. Pairs of *Eleutherodactylus* often were observed in amplexus for several hours in the forest. Frequently, the female of the amplectant pair still had not ovulated the following day (observed by dissection). On the other hand, females of most hylids which breed in congregations do not come to the breeding site until they have ovulated. Much less time is spent in amplexus for these species than for *Eleu-*

therodactylus. It is suggested that ovulation before entering the breeding site is a behavioral adaptation reducing vulnerability of the pair to potential predators. The chance of a predator encountering an amplectant pair of tree frogs at an aquatic site amidst a large congreation of calling individuals is perhaps greater than that of a predator encountering a pair of *Eleutherodactylus* isolated in the forest. *Bufo marinus* is an exception; although the species congregates and breeds in ditches in open areas, pairs often remain in amplexus for several hours (and up to six days in captivity). Possible reasons they are able to afford this behavior are their toxic skin secretions and large size; *B. marinus* probably has very few natural predators. *Phyllomedusa,* which also have poisonous skin secretions, remain in amplexus at breeding sites for several hours.

Energy allotted to reproduction ("reproductive effort") is partitioned differentially for each species among egg production, sperm production, courtship, vocalization, territoriality, parental care, frequency of breeding, and nest-building. Members of mode 1 represent the simplest situation. Males congregate at aquatic breeding sites and call. Some species call continuously even though there may be no water present and females are not present at the site; males of other species call only following heavy rains. The reproductive energy allotment of males is divided into sperm production and calling, for there is no apparent courtship, territoriality, or parental care involved. The reproductive energy of females is channeled into egg production. It is not known how frequently individuals breed, but based on the immature complement found in nearly every gravid female, it is suggested that females breed repeatedly throughout the year.

Hyla boans represents a slightly more complicated situation. Males expend energy calling, constructing nests, and possibly defending the nests. Females take no part in these activities, but put energy into a relatively large egg clutch.

Frogs that deposit eggs on vegetation above water probably expend more energy in choosing oviposition sites than do frogs of mode 1 type of reproduction. Some species (such as *Hyla bokermanni* and *H. sarayacuensis*) deposit eggs in many small clutches, spread out on several leaves, probably requiring more energy than single oviposition. It is assumed that reproductive energy for most species is spent in calling, sperm and egg production, and searching for oviposition sites. Male *Phyllomedusa tarsius* expend energy in folding leaves around the egg clutch. Some of the energy allotment of the female is used in the production of empty gelatinous capsules, probably formed in the oviduct.

Males of the species that produce foam nests (modes 5 and 7) spend energy in constructing the nest during amplexus, in addition to the energy used in calling. Aggressive behavior has been reported for leptodactylids (Brattstrom and Yarnell, 1968), but was not observed in any of the species at Santa Cecilia. Reproductive energy in the female is channeled into egg production. *Leptodactylus andreae* produces few, large eggs, each one representing a large energy investment. The eggs of *Leptodactylus mystaceus,* likewise, are relatively large, but fecundity is much greater for this species than for the former, relative to body size.

The dendrobatids represent a more complex situation. It is probable that (at least for *Dendrobates*) elaborate courtship and territoriality are important aspects of the breeding process. These have been described for several dendrobatids (Crump, 1972; Duellman, 1966; Goodman, 1971; Sexton, 1960; Silverstone, 1973; Test, 1954; Wardenier, 1973). From my studies on *Dendrobates granuliferus* in Costa Rica (Crump, 1972), I concluded that territoriality is an energetically expensive activity in high density populations based on the

frequency of observed encounters. Territories are defended by physical combat lasting up to several minutes. Courtship is elaborate and probably costly in energy. Much time (and energy) is spent by the female searching for an appropriate oviposition site. However, in *Dendrobates auratus* the male chooses the site (Wardenier, 1973). No courtship activity or territoriality was observed for the five species at Santa Cecilia, but combat activity has been observed between male *Dendrobates pictus* in Perú (C. Toft, personal communication). Males call but do not congregate. It is assumed that the tadpoles of all five species are transported to water on the dorsum of the males or females. This form of parental care potentially requires much energy on the part of either sex. Fecundity is low, and the eggs are heavily yolked and large.

The strategy of the 14 species of *Eleutherodactylus* is the production of a few, large eggs. Presumably each egg is energetically costly. The eggs are deposited in relatively protected areas (e.g., amidst leaf litter and under tree bark). Males call but do not congregate. No parental care or elaborate courtship was observed; in captivity, males mount the females in simple amplexus, without preliminary courtship.

Eggs and Larvae in the Aquatic Environment.—The egg stage probably is more vulnerable to predators than the tadpole or adult stages because eggs are immobile, and therefore unable to escape predators. At Santa Cecilia members of five of the eight families show some means of protecting eggs rather than depositing them in open bodies of water. These adaptations (e.g., eggs deposited on vegetation above water, in foam nests, on land) undoubtedly have arisen independently. However, upon hatching, the tadpoles are left to fend for themselves in the aquatic environment, and are dependent on it until metamorphosis.

Chief predators on anuran eggs are aquatic insects, fish, and snakes. Several studies have been carried out in order to examine the effects of anuran eggs on predators. Licht (1968, 1969) demonstrated that eggs of several species of *Bufo* were unpalatable and toxic when ingested by potential vertebrate and invertebrate predators. Licht (1969) found that eggs of *Rana* and *Hyla*, however, were palatable and nontoxic to the same potential predators. Grubb (1972) examined differential predation of fish (*Gambusia*) on the eggs of *Acris, Bufo, Gastrophryne, Hyla, Pseudacris, Scaphiopus,* and *Rana.* None of the eggs seemed to have toxic effects on the fish. Grubb found that the fish ate a significantly larger number and greater volume of eggs of those species that generally breed in temporary as opposed to permanent water. His explanation for this is that species that deposit eggs in temporary water generally have less firm gelatinous capsules. Aquatic predators (especially fish) are more abundant in permanent water than in temporary water. Perhaps the firmer egg capsule typical of permanent water breeders serves as a mechanical defense against predators.

The relationship between egg pigmentation and the aquatic environment is not intuitively obvious. The melanin of eggs may promote absorption of radiant heat energy and/or shield the eggs from ultraviolet radiation. In either case, those eggs exposed to light are pigmented, whereas those sheltered from direct sunlight generally lack pigment. Species that deposit eggs in shallow bodies of water (e.g., *Bufo marinus, Hyla lanciformis, H. marmorata, H. rubra*) have heavily pigmented eggs. The melanin likely promotes more rapid development in the warm water, and thus is a selective advantage in temporary habitats.

There are far fewer species of frogs that breed in the large, permanent bodies of water at Santa Cecilia than in the smaller, ephemeral and temporary environments. One explanation is related to potential predator pressure. The per-

manent aquatic habitats at Santa Cecilia are deep, and fish are abundant. The temperature of the water is much cooler than that of small aquatic sites. Because rate of development is directly related to water temperature, perhaps there is a penalty for breeding where development is less rapid and eggs and tadpoles are exposed to predators for a greater length of time. Most of the species that breed in permanent water have large egg clutches, possibly a preadaptation to high egg and larval mortality.

There is no significant difference in fecundity, intraoval developmental time, or hatchling size between species that deposit eggs in ephemeral or temporary water and those that deposit eggs in more permanent water. This is probably the result of balancing hazards. In other words, neither environment may be inherently more advantageous than the other. In the temporary environment, the greatest hazard probably is unpredictability of the life span of the habitat, whereas in the more permanent habitat, it is probably the greater number of aquatic predators.

SUMMARY AND CONCLUSIONS

Eighty-one species of frogs representing ten modes of reproduction (defined as a combination of type of development and oviposition site) are known from Santa Cecilia, Ecuador. The study site is in an aseasonal environment in the upper Amazon Basin. Several explanations are offered for the extremely rich anuran fauna. Paleoclimatic unstability may account for the extensive speciation which occurred in the lowland tropics of South America. The diversity of reproductive modes probably represents adaptive responses to changing environments.

There are many reproductive strategies operant in the anuran community. Some species put all their reproductive energy allotted into egg and sperm production and vocalization. Other species expend energy for constructing nests, courtship, territoriality, and parental care. Some species produce a few large eggs presumably high in energy content, others distribute energy through thousands of small eggs. Species that deposit many eggs directly in water (*r*-strategists) generally breed in unpredictable, ephemeral or temporary environments. The *K*-strategists are those species that are completely independent of open bodies of water; they deposit terrestrial or arboreal eggs which have direct development. The breeding sites of the latter species are considered to be more predictable and less hazardous than those of the former.

Approximately 46 per cent of the species of frogs deposit eggs directly in water; the remainder have specialized oviposition sites and/or direct development. Many of these species have specialized behavioral and/or morphological adaptations toward terrestriality. Behavioral modifications include construction of a basin in the mud for egg deposition, oviposition on vegetation above water, production of a foam nest in which the eggs are suspended, and oviposition on land with subsequent carrying of the tadpoles to water on the dorsum of the adults. Morphological modifications include prepollical spines and horny nuptial excrescences that presumably aid in grasping the female during amplexus. Generally those species that deposit eggs in exposed situations have pigmented eggs, whereas species that deposit eggs in sheltered sites have eggs lacking pigment. Hatchling *Eleutherodactylus* have "egg teeth" (horny projections on the tip of the snout) used in ripping the jelly capsule of the nonaquatic egg during hatching. Juvenile *Hemiphractus proboscideus* presumably are attached to the dorsum of the female by flat gills.

The premise on which this study is based is that because the number of aquatic breeding sites is less than the number of species, the sites represent a potentially limiting resource. Spatial and temporal utilization of the sites was

examined. The data support the suggestion that the reproductive diversity at Santa Cecilia enables the coexistence of many species through partitioning of breeding sites. Eight aquatic breeding sites in three major environments (forest, forest-edge, and open disturbed areas) were studied. Forty-one species were found breeding at these sites. Some species are specialists, breeding only in a restricted variety of sites; others are habitat generalists, breeding in all three environments. No species was found breeding in all eight sites. The maximum number of species breeding at any site throughout the year was 14, but the maximum number breeding synchronously at any given site was ten. It is concluded that the pattern of spatial distribution is probably the result of both physical requirements and biotic interactions. Species are grouped into three categories based on annual reproductive activity: continuous, opportunistic, and sporadic breeders.

Each species possesses a unique complement of reproductive characteristics. The following conclusions resulted from an extensive examination of quantifiable variables.

1.—Only 11 of 41 species (26.8%) demonstrate significant positive correlations between snout-vent length and number of mature ovarian eggs.

2.—Within each of three reproductive modes tested (eggs in water, eggs on vegetation above water, and nonaquatic eggs with direct development), there is a significant positive correlation between snout-vent length and fecundity.

3.—There is significant between-month variation in both snout-vent length and fecundity for *Eleutherodactylus variabilis* and *Hyla rubra*. *Eleutherodactylus croceoinguinis* shows significant monthly variation in snout-vent length; both *Eleutherodactylus lanthanites* and *Hyla parviceps* demonstrate significant monthly variation in fecundity. There is no significant between-month variation in either variable in *Dendrobates parvulus*. Variation is not correlated with rainfall; no explanation is suggested by the data.

4.—There is a significant positive correlation between snout-vent length and volume (23 species).

5.—There is a significant positive correlation between body volume and volume of the mature ovarian complement (23 species).

6.—The range in clutch volume expressed as a percentage of the total volume is 3.1 to 18.2 (23 species). A negative trend indicates that as snout-vent length increases, proportionately less of the total volume is accounted for by the egg mass.

7.—Females are significantly larger than males in 59 of the 61 species examined. There is no significant sexual dimorphism in size in *Hyla boans* and *Hyla punctata*.

8.—There is no significant correlation between either female snout-vent length or body volume and sexual dimorphism in size. Likewise, there is no significant correlation between fecundity and dimorphism in size. It is concluded that sexual dimorphism in size is determined more by evolutionary (taxonomic) relationships than by reproductive variables.

9.—There is no apparent assortative mating based on size in the four species tested (*Hyla garbei, Eleutherodactylus altamazonicus, Eleutherodactylus croceoinguinis,* and *Eleutherodactylus variabilis*).

10.—For those species that deposit eggs in water, there is a trend of larger ovum size with larger clutch size. This trend is not evident for those species that deposit eggs on vegetation above water.

11.—Species that deposit eggs on vegetation above water take longer to develop and hatch than those that deposit eggs in water; the hatchlings are generally larger in the former group (4.2 to 12.6 mm versus 3.8 to 6.0 mm in the latter group).

12.—Within 22 species of the genus *Hyla*, species that deposit eggs in water

have a significantly higher egg mass relative to body length than do those species that deposit eggs on vegetation above water. Mean ovarian size factors for the two groups are 20.47 (15 species) and 11.08 (7 species).

13.—Among the species tested (all deposit eggs in water), fecundity is not significantly greater for those species that breed in "temporary" environments (4 species) versus "permanent" environments (8 species). Likewise, there is no significant difference in either intraoval developmental time or hatchling size between the two environments.

14.—The greatest variation in the reproductive variables examined occurs among those species that deposit eggs in water (other than tree holes or constructed nests). The least variation is found in species that deposit terrestrial eggs and transport the tadpoles to water.

RESUMEN Y CONCLUSIONES

Se conocen 81 especies de ranas en Santa Cecilia, Ecuador, las mismas se agrupan en 10 modos reproductivos (estos se definen combinando el tipo de desarrollo y sitio donde los huevos son puestos). El sitio donde se hizo el estudio es un ambiente no estacional ubicado en la Cuenca Alto Amazónica. Se dan varias explicaciones sobre la extremada riqueza de la fauna de anuros en esta localidad. La inestabilidad paleoclimática pudo haber causado la extensa especiación que ha tenido lugar en las partes bajas del trópico de Sur América. La diversidad de modos reproductivos probablemente coevolucionó con la fauna, como una adaptación a los cambios ambientales.

Varias estrategias reproductivas operan en la comunidad de anuros. Algunas especies utilizan toda su energía destinada para reproducirse en la producción de huevos y espermatozoides, y en el canto nupcial. Otras especies utilizan la energía en la construcción de nidos, cortejo, territorialidad y cuidado parental. Algunas especies producen pocos huevos grandes, presumiblemente ricos en contenido energético; otras usan la energía para producir gran cantidad de huevos pequeños. Aquellas especies que depositan sus huevos directamente en el agua (seleccionadas en "r") generalmente se reproducen en ambientes no pronosticables, efímeros o temporales. Las seleccionadas en "K" son aquellas especies que son completamente independientes del agua; ellas depositan huevos que se desarrollan directamente en la tierra o en los árboles. Estos sitios se consideran más pronosticables y menos sometidos al azar que los temporales.

Aproximadamente 46 por ciento de las especies depositan sus huevos directamente en el agua; el resto tiene sitios especiales para poner y/o desarrollo directo. Muchas de estas especies tienen conducta especial y/o adaptaciones morfológicas que indican tendencia hacia la terrestrialidad. Las modificaciones en conducta incluyen estrategias tales como la construcción de una depresión en el barro donde se depositan los huevos, posturas en la vegetación sobre el agua, construcción de un nido de espuma en el cual suspenden los huevos, y postura de los huevos en la tierra desde donde los renacuajos son llevados al agua en el dorso de los adultos. Las modificaciones morfológicas incluyen espinas y excrescencias callosas en el dedo interno de las manos; éstas presumiblemente ayudan el macho a sostener la hembra durante el amplexo. Generalmente las especies que ponen en lugares expuestos tienen huevos pimentados; mientras que aquellas que los depositan en lugares protegidos no muestran pigmentación alguna. Las *Eleutherodactylus* recien eclosionaclos tienen "dientes de huevo" (estructuras duras en la punta del hocico) que usan para romper la cápsula gelatinosa durante el proceso de la eclosión. Los juveniles de la especie *Hemiphractus proboscideus* presumiblemente se pegan al dorso de la hembra mediante branquias.

Este estudio se basa en la siguiente

suposición: debido a que el número de sitios para la reproducción acuática es menor que el número de especies, ellos representan un recurso potencialmente limitado. Se examinó la utilización espacial y temporal de estos sitios. Los datos que se dan sugieren que la diversidad reproductiva en Santa Cecilia garantiza la coexistencia de muchas especies mediante el reparto de los sitios de reproducción. Se estudiaron ocho sitios acuáticos de reproducción en tres ambientes generales (bosque, orilla de bosque, áreas abiertas disturbadas). Se encontraron 41 especies reproduciéndose en estos sitios. Algunas especies se especializan en reproducirse en una variedad restringida de sitios; otras son de hábitos más generales y pueden reproducirse en los tres ambientes. No se encontró ninguna especie que se reprodujera en los ocho sitios. El máximo número de especies que se encontró reproduciéndose a través del año en un sitio dado fué de 14, pero el máximo número actuando al mismo tiempo fué de 10. Se concluye que la distribución espacial probablemente es el resultado tanto de los requerimientos físicos como de las interacciones bióticas. Las diferentes especies se agrupan en tres categorías de acuerdo a la actividad reproductiva anual; reproductores contínuos, oportunísticos, y esporádicos.

Cada especie pose un complemento único de parámetros reproductivos. Se pueden sacar las siguientes conclusiones despues de examinar las variables cuantitativas:

1.—En la mayoría de las especies no parece tener ninguna ventaja selectiva el destinar gran cantidad de energía para crecer, y aumentar asi la fecundidad. Solo 11 de 41 especies (26,8%) mostraron correlaciones positivas significativas entre la longitud ano-hocico y el número huevos ováricos maduros.

2.—Dentro de cada uno de los tres modos reproductivos que se probaron (huevos en el agua, huevos en vegetación sobre el agua, y huevos no acuáticos con desarrollo directo), hay una correlación positiva significativa entre la longitud ano-hocico y la fecundidad.

3.—En *Eleutherodactylus variabilis* e *Hyla rubra* hay una variación entre mensual significativa en la longitud ano-hocico y fecundidad. *Eleutherodactylus croceoinguinis* muestra una variación mensual significativa en la longitud ano-hocico; tanto *Eleutherodactylus lanthanites* como *Hyla parviceps* monstraron una variación mensual significativa en fecundidad. No hay variación entre mensual significativa en ninguna variable en *Dendrobates parvulus*. La variación no está correlacionada con la cantidad de lluvias; los datos no ofrecen ninguna explicación.

4.—Hay una correlación positiva significativa entre la longitud ano-hocico y el volumen (23 especies).

5.—Hay una correlación positiva significativa entre el volumen corporal y el volumen del complemento ovárico maduro (23 especies).

6.—La variación en el número de los huevos, expresada como un porcentaje del volumen total es de 3,1 a 18,2 (23 especies). Una tendencia negativa indica que cuando la longitud ano-hocico aumenta, proporcionalmente menos del volumen pertenece a la masa de huevos.

7.—Las hembras son significativamente más grandes que los machos en 59 de las 61 especies examinadas. No hay dimorfismo sexual significativo en el tamaño de *Hyla boans* e *Hyla punctata*.

8.—No hay correlación significativa entre la longitud ano-hocico o el volumen corporal de la hembra y el dimorfismo sexual en tamaño. De la misma manera, no hay correlación significativa entre la fecundidad y el dimorfismo sexual en tamaño. Se concluye que el dimorfismo sexual en tamaño está determinado más por las relaciones evolutivas (taxonómicas) que por los parámetros reproductivos.

9.—No hay apareamiento determinado en relación al tamaño en las cuatro especies que se probaron (*Hyla garbei, Eleutherodactylus altamazonicus, Eleu-*

therodactylus croceoinguinis, y *Eleuterodactylus variabilis*).

10.—Las especies que depositan sus huevos en el agua tienden a tener óvulos grandes y en gran cantidad. Esta tendencia no es evidente en aquellas especies que depositan sus huevos en vegetación sobre el agua.

11.—Los huevos de las especies que depositan sus complementos en vegetación sobre el agua toman más tiempo en desarrollarse y eclosionar que aquellas que los depositan en el agua; las larvas recién eclosionaclas son generalmente más grandes en el primer grupo (4,2 a 12,6 mm versus 3,8 a 6,0 en el último grupo).

12.—De 22 especies del género *Hyla*, aquellas que depositan sus huevos en el agua tienen una masa de huevos significativamente más grande en relación a la longitud del cuerpo que aquellas que los depositan en vegetación sobre el agua. Las medianas de los factores del tamaño ovárico para los dos grupos son 20,47 (15 especies) y 11,08 (7 especies), respectivamente.

13.—Entre las especies probadas (todas depositan los huevos en el agua), la fecundidad no es significativamente más grande en aquellas especies que se reproducen en ambientes "temporales" (4 especies) versus ambientes "permanentes" (8 especies). Asi mismo, no hay diferencia significativa en el tiempo de desarrollo del huevo o el tamaño de la larva recién eclosionada entre los dos ambientes.

14.—La mayor variación de los parámetros reproductivos examinados se encuentra entre aquellas especies que depositan sus huevos en el agua (se excluyen aquellas que los depositan en cavidades en los árboles o las que construyen sus nidos). La menor variación se encuentra en las especies que depositan sus huevos lejos del agua y luego los renacuajos son llevados a ésta.

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Appendix 1

Reproductive Modes of 81 Species of Frogs at Santa Cecilia, Ecuador. (An * indicates the species was not observed during my study; P indicates presumed reproductive mode.)

1. Eggs deposited in ditches, puddles, swamps, ponds, lakes, and streams; tadpoles in water.
   1. *Ceratophrys calcaratus**
   2. *Bufo glaberrimus*
   3. *Bufo marinus*
   4. *Bufo typhonius*
   5. *Dendrophryniscus minutus*
   6. *Hyla alboguttata* (P)
   7. *Hyla calcarata*
   8. *Hyla cruentomma*
   9. *Hyla fasciata*
   10. *Hyla funerea*
   11. *Hyla garbei*
   12. *Hyla geographica*
   13. *Hyla granosa*
   14. *Hyla lanciformis*
   15. *Hyla marmorata*
   16. *Hyla minuta*
   17. *Hyla parviceps*
   18. *Hyla punctata*
   19. *Hyla rhodopepla*
   20. *Hyla riveroi*
   21. *Hyla rossalleni**
   22. *Hyla rubra*
   23. *Osteocephalus buckleyi*
   24. *Osteocephalus leprieurii*
   25. *Osteocephalus taurinus*
   26. *Phrynohyas coriacea*
   27. *Sphaenorhynchus eurhostus**
   28. *Sphaenorhynchus carneus*
   29. *Chiasmocleis anatipes*
   30. *Chiasmocleis bassleri* (P)
   31. *Chiasmocleis ventrimaculata* (P)
   32. *Ctenophryne geayi** (P)
   33. *Hamptophryne boliviana*
   34. *Rana palmipes*
2. Eggs deposited in tree cavity above ground; tadpoles develop there.
   1. *Nyctimantis rugiceps* (P)
3. Eggs deposited in constructed basin of water on ground; tadpoles develop there.
   1. *Hyla boans*
4. Eggs deposited on vegetation above water; tadpoles hatch and fall into water where they develop.
   1. *Centrolenella midas*
   2. *Centrolenella munozorum*
   3. *Centrolenella resplendens**
   4. *Hyla favosa*
   5. *Hyla leucophyllata*
   6. *Hyla sarayacuensis*
   7. *Hyla triangulum*
   8. *Hyla bifurca*
   9. *Hyla bokermanni*
   10. *Hyla brevifrons*
   11. *Phyllomedusa palliata*
   12. *Phyllomedusa tarsius*
   13. *Phyllomedusa tomopterna*
   14. *Phyllomedusa vaillanti*
5. Eggs deposited in foam nest either on or near water; tadpoles develop in water.
   1. *Leptodactylus discodactylus*
   2. *Leptodactylus mystaceus*
   3. *Leptodactylus pentadactylus*
   4. *Leptodactylus rhodomystax**
   5. *Leptodactylus wagneri*
   6. *Physalaemus petersi*
6. Eggs deposited on land; tadpoles carried to water by parent—development occurs in water.
   1. *Colostethus marchesianus*
   2. *Colostethus sauli*
   3. *Dendrobates parvulus*
   4. *Dendrobates pictus*
   5. *Phyllobates femoralis*
7. Eggs deposited in foam nest on land; tadpoles develop in nest.
   1. *Leptodactylus andreae*
8. Eggs deposited out of water; direct development.
   1. *Eleutherodactylus acuminatus*
   2. *Eleutherodactylus altamazonicus*
   3. *Eleutherodactylus conspicillatus*
   4. *Eleutherodactylus croceoinguinis*
   5. *Eleutherodactylus diadematus*
   6. *Eleutherodactylus lacrimosus*
   7. *Eleutherodactylus lanthanites*
   8. *Eleutherodactylus martiae*
   9. *Eleutherodactylus ockendeni*
   10. *Eleutherodactylus paululus*
   11. *Eleutherodactylus pseudoacuminatus*
   12. *Eleutherodactylus quaquaversus*
   13. *Eleutherodactylus sulcatus*
   14. *Eleutherodactylus variabilis*
9. Eggs and young buried in skin pits on dorsum of female; direct development—aquatic.
   1. *Pipa pipa**
10. Eggs and young attached to dorsum of female by "gills"; direct development—terrestrial.
    1. *Hemiphractus proboscideus*
11. Mode of reproduction unknown.
    1. *Edalorhina perezi*
    2. *Ischnocmena quixensis*
    3. *Lithodytes lineatus*

Appendix 2

Species Names Corresponding to Numbers Utilized in Community Matrices (Tables 4-5) and Breeding Site Table (Appendix 3).

1 *Leptodactylus mystaceus*
2 *Bufo marinus*
3 *Hamptophryne boliviana*
4 *Rana palmipes*
5 *Sphaenorhynchus carneus*
6 *Hyla calcarata*
7 *Hyla cruentomma*
8 *Hyla funerea*
9 *Hyla garbei*
10 *Hyla geographica*
11 *Hyla granosa*
12 *Hyla lanciformis*
13 *Hyla marmorata*
14 *Hyla parviceps*
15 *Hyla punctata*
16 *Hyla rhodopepla*
17 *Hyla rubra*
18 *Hyla bifurca*
19 *Hyla bokermanni*
20 *Hyla brevifrons*
21 *Hyla leucophyllata*
22 *Hyla sarayacuensis*
23 *Hyla triangulum*
24 *Phyllomedusa palliata*
25 *Phyllomedusa tarsius*
26 *Phyllomedusa tomopterna*

Appendix 3

Breeding Sites of 26 Species with Aquatic Larvae. See Appendix 2 for species names. The sites are as follows: Air Strip Edge Ditches, A.S.E.D.; Clearing Swamp, C.S.; Forest Edge Swamp A, F.E.S.A.; Forest Edge Swamp B, F.E.S.B.; Heliconia Swamp, H.S.; Second-Growth Forest Swamp, S.G.F.S.; Palm Pond, P.P.; Lake, L.

Species		A.S.E.D.	C.S.	F.E.S.A.	F.E.S.B.	H.S.	S.G.F.S.	P.P.	L.	Tot. No. Sites
1	----	×	—	×	×	—	—	—	—	3
2	----	×	—	—	—	—	—	—	—	1
3	----	—	—	×	—	×	—	×	—	3
4	----	×	×	—	—	—	—	×	—	3
5	----	—	—	—	—	—	—	×	—	1
6	----	—	—	—	—	—	×	—	×	2
7	----	—	—	×	×	×	×	×	—	5
8	----	—	—	×	—	×	—	×	—	3
9	----	×	×	×	×	×	—	—	—	5
10	----	—	—	—	—	—	—	—	×	1
11	----	—	—	—	—	—	×	—	×	2
12	----	×	×	×	×	—	—	—	—	4
13	----	×	—	—	×	×	—	—	—	3
14	----	—	—	×	×	×	—	×	—	4
15	----	—	×	—	—	—	×	×	—	3
16	----	—	×	×	×	×	×	×	—	6
17	----	×	×	×	×	—	—	—	—	4
18	----	×	×	—	×	—	—	—	—	3
19	----	—	×	×	—	×	×	×	—	5
20	----	—	—	×	—	×	—	—	—	2
21	----	—	—	×	—	—	×	—	—	2
22	----	—	×	×	×	×	—	×	—	5
23	----	×	×	×	×	—	—	—	×	5
24	----	—	—	—	×	×	—	×	—	3
25	----	—	—	—	×	×	—	×	—	3
26	----	—	—	—	—	—	—	×	—	1
Total Breeding Species		9	10	14	13	12	7	13	4	

Appendix 4

Number of Females and Percent Gravid Individuals Found Per 20-Day Time Period. The top line indicates the total number of females found and the number beneath, the percent gravid.

Species	20-Day Time Blocks																				N Females / N Gravid	Per Cent Gravid
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
E. acuminatus	---	---	1	---	---	1	---	---	---	---	---	---	---	---	---	---	3	---	---	---	5/4	80.0%
	---	---	100%	---	---	0%	---	---	---	---	---	---	---	---	---	---	100%	---	---	---		
E. altamazonicus	---	---	---	6	1	2	---	1	---	---	---	---	1	---	2	1	2	---	---	---	16/14	87.5%
	---	---	---	100%	100%	100%	---	100%	---	---	---	---	0%	---	50%	100%	100%	---	---	---		
E. conspicillatus	---	3	---	2	---	---	1	---	---	---	---	---	---	---	4	2	2	---	---	---	14/8	57.1%
	---	66.7%	---	50%	---	---	0%	---	---	---	---	---	---	---	50%	100%	100%	---	---	---		
E. croceoinguinis	2	---	---	5	---	3	3	1	1	2	9	8	8	9	20	7	16	2	3	---	99/88	88.9%
	100%	---	---	80%	---	100%	100%	100%	0%	50%	77.8%	87.5%	87.5%	77.8%	95%	85.7%	100%	100%	100%	---		
E. diadematus	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1/1	100%
	100%	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
E. lacrimosus	---	---	1	---	3	---	---	---	---	---	---	---	1	---	---	---	---	---	---	---	5/5	100%
	---	---	100%	---	100%	---	---	---	---	---	---	---	100%	---	---	---	---	---	---	---		
E. lanthanites	3	3	3	5	1	---	4	1	2	---	3	4	6	3	24	4	13	4	4	---	87/70	80.5%
	100%	100%	100%	80%	0%	---	25%	0%	100%	---	100%	100%	83.3%	100%	75%	100%	76.9%	100%	75%	---		
E. martiae	---	1	1	3	1	1	1	2	---	---	2	---	3	1	---	---	2	1	---	---	19/14	73.3%
	---	100%	100%	33.3%	100%	100%	100%	100%	---	---	100%	---	66.7%	0%	---	---	50%	100%	---	---		
E. ockendeni	1	2	4	4	1	3	---	1	---	---	---	---	6	2	3	---	2	1	---	---	30/18	60.0%
	0%	100%	100%	50%	0%	33.3%	---	0%	---	---	---	---	33.3%	100%	100%	---	100%	0%	---	---		
E. paululus	---	---	---	1	---	---	---	---	---	---	---	---	---	1	---	---	---	---	---	---	2/1	50.0%
	---	---	---	0%	---	---	---	---	---	---	---	---	---	100%	---	---	---	---	---	---		
E. pseudoacuminatus	---	---	---	1	---	---	---	1	1	---	---	1	2	1	---	2	1	---	---	---	10/8	80.0%
	---	---	---	100%	---	---	---	0%	100%	---	---	100%	100%	100%	---	50%	100%	---	---	---		
E. quaquaversus	---	---	---	---	2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	2/1	50.0%
	---	---	---	---	50%	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
E. variabilis	3	5	8	13	14	17	11	9	11	5	6	26	17	23	9	5	17	16	7	---	222/155	69.8%
	100%	60%	75%	46.1%	42.8%	70.6%	72.7%	44.4%	45.5%	60%	83.3%	65.4%	100%	82.6%	77.8%	100%	64.7%	87.5%	57.1%	---		
I. quixensis	1	3	2	1	2	---	---	3	1	---	1	3	2	---	2	1	3	1	1	---	27/23	74.2%
	100%	100%	100%	100%	50%	---	---	66.7%	100%	---	0%	66.7%	100%	---	100%	100%	100%	100%	100%	---		
L. andreae	---	---	---	2	1	1	1	---	---	---	---	4	---	---	---	---	---	---	---	---	9/5	55.6%
	---	---	---	100%	100%	0%	0%	---	---	---	---	50%	---	---	---	---	---	---	---	---		
L. discodactylus	1	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	2/2	100%
	100%	100%	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
L. mystaceus	---	1	---	---	2	1	3	4	---	1	---	5	2	1	1	1	1	---	---	---	23/16	69.6%
	---	100%	---	---	0%	100%	66.7%	75%	---	0%	---	100%	100%	100%	0%	0%	100%	---	---	---		

L. wagneri	---	---	---	---	---	---	---	---	---	---	---	---	---	1 100%	---	---	---	---	---	---	---	1/1	100%
B. marinus	---	1 100%	---	2 100%	---	1 100%	---	---	---	---	---	---	---	1 100%	---	---	---	---	---	---	---	5/5	100%
B. typhonius	2 50%	2 100%	3 66.7%	---	---	1 100%	---	---	1 100%	---	---	1 100%	---	2 100%	---	1 100%	4 75%	1 0%	---	---	---	18/14	77.8%
D. minutus	3 33.3%	8 37.5%	4 25%	---	4 50%	1 0%	5 20%	4 0%	---	6 33.3%	3 66.7%	5 80%	4 100%	4 75%	3 100%	6 83.3%	13 69.2%	---	1 100%	---	---	74/41	55.4%
C. marchesianus	3 100%	3 66.7%	2 50%	---	---	2 100%	---	---	---	---	3 100%	1 100%	1 100%	3 100%	11 100%	2 100%	10 90%	---	2 100%	---	---	43/40	93.0%
C. sauli	---	---	1 100%	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1/1	100%
D. parvulus	12 100%	3 100%	2 100%	3 100%	3 100%	8 100%	4 75%	4 100%	---	3 100%	3 100%	10 100%	8 100%	8 100%	9 88.9%	7 85.7%	19 94.7%	4 100%	3 100%	---	---	113/109	96.4%
D. pictus	---	1 0%	1 100%	2 100%	3 100%	10 80%	5 100%	---	---	---	---	5 100%	7 85.7%	8 100%	1 100%	3 100%	2 100%	1 100%	3 100%	---	---	52/48	92.3%
P. femoralis	1 0%	1 100%	2 100%	---	---	1 100%	---	1 100%	---	---	---	---	---	---	---	---	---	---	---	---	---	6/5	83.3%
H. alboguttata	1 100%	2 100%	1 100%	2 100%	6 50%	10 40%	1 0%	---	1 0%	1 0%	---	5 100%	---	---	3 100%	---	---	1 0%	---	---	---	34/21	61.8%
H. bifurca	---	1 100%	1 100%	1 100%	2 50%	2 100%	1 100%	2 100%	---	---	---	---	---	1 100%	---	---	---	1 0%	1 100%	1 100%		14/12	85.7%
H. boans	---	---	1 100%	---	---	---	2 100%	---	---	1 100%	---	1 100%	---	---	---	---	---	---	---	---	---	5/5	100%
H. bokermanni	---	---	1 0%	---	---	1 100%	3 100%	2 100%	---	1 100%	---	2 100%	23 100%	25 92%	22 86.4%	3 100%	6 83.3%	2 100%	1 100%	---	---	92/85	92.4%
H. brevifrons	---	1 100%	1 0%	---	---	1 0%	3 100%	1 0%	2 100%	1 100%	---	---	1 100%	1 100%	---	---	---	---	1 100%	---	---	13/10	76.9%
H. calcarata	1 0%	---	---	1 0%	1 100%	2 50%	2 50%	1 100%	---	---	---	---	1 100%	1 100%	1 100%	---	---	---	---	---	---	11/7	63.6%
H. cruentomma	---	---	---	---	---	---	---	---	1 0%	---	1 0%	2 100%	1 100%	2 100%	---	---	2 50%	---	---	2 100%		11/8	72.7%
H. fasciata	1 0%	1 0%	3 100%	3 33.3%	1 100%	1 100%	1 0%	---	1 0%	1 100%	1 0%	4 75%	3 66.7%	2 100%	4 100%	3 100%	3 100%	---	3 66.7%	---	---	36/27	75.0%
H. funerea	1 0%	1 0%	---	---	100%	---	---	---	---	---	1 100%	---	2 100%	1 100%	2 100%	1 0%	1 100%	---	---	1 100%		12/9	75.0%
H. garbei	---	1 100%	---	2 50%	3 66.7%	8 75%	2 100%	---	---	1 100%	---	2 100%	1 100%	1 100%	3 66.7%	4 100%	4 100%	9 77.8%	3 100%	3 100%		47/40	85.1%
H. geographica	---	---	---	2 50%	3 33.3%	---	2 50%	1 100%	---	---	---	---	1 0%	---	2 50%	---	---	---	---	---		11/5	45.5%

Appendix 4—*Concluded*

Species	20-Day Time Blocks																				N Females / N Gravid	Per Cent Gravid
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
H. granosa	---	---	1	---	---	---	---	---	---	---	---	---	1	2	---	1	---	---	---	---	5/5	100%
	---	---	100%	---	---	---	---	---	---	---	---	---	100%	100%	---	100%	---	---	---	---		
H. tanciformis	1	---	5	1	1	2	1	1	---	---	---	---	6	4	1	---	3	---	---	2	28/24	85.7%
	100%	---	100%	0%	100%	100%	100%	100%	---	---	---	---	83.3%	75%	100%	---	100%	---	---	50%		
H. Teucophyllata	---	---	---	---	---	1	2	---	---	---	---	---	---	---	---	---	---	---	1	---	4/4	100%
	---	---	---	---	---	100%	100%	---	---	---	---	---	---	---	---	---	---	---	100%	---		
H. marmorata	---	---	---	---	---	3	---	---	---	1	---	---	3	---	---	---	---	---	---	---	7/6	85.7%
	---	---	---	---	---	100%	---	---	---	100%	---	---	66.7%	---	---	---	---	---	---	---		
H minuta	---	3	1	---	---	---	---	---	---	---	---	---	---	---	---	---	2	---	---	---	6/5	83.3%
	---	100%	100%	---	---	---	---	---	---	---	---	---	---	---	---	---	50%	---	---	---		
H. parviceps	1	6	10	12	13	22	8	9	2	7	3	10	12	15	2	1	2	1	5	5	146/125	85.6%
	0%	83.3%	40%	75%	84.6%	95.4%	87.5%	77.8%	100%	100%	100%	100%	91.7%	86.7%	100%	100%	100%	0%	100%	100%		
H. punctata	---	---	---	1	1	2	1	1	---	---	---	---	---	---	3	3	1	2	4	1	20/18	90.0%
	---	---	---	0%	0%	100%	100%	100%	---	---	---	---	---	---	100%	100%	100%	100%	100%	100%		
H. rhodopepla	---	5	---	1	---	6	15	12	4	3	---	1	5	10	5	1	4	1	21	20	114/112	98.2%
	---	80%	---	0%	---	100%	100%	100%	100%	100%	---	100%	100%	100%	100%	100%	100%	100%	100%	100%		
H. rubra	3	2	---	3	1	13	1	16	---	1	3	2	9	4	---	---	9	---	8	5	80/71	88.8%
	100%	100%	---	66.7%	100%	84.6%	100%	75%	---	100%	100%	100%	100%	100%	---	---	100%	---	75%	100%		
H. sarayacuensis	---	---	---	---	1	2	1	1	---	---	---	---	3	5	2	---	2	---	1	---	18/16	88.9%
	---	---	---	---	0%	100%	100%	0%	---	---	---	---	100%	100%	100%	---	100%	---	100%	---		
H. triangulum	---	2	---	---	---	2	2	3	---	2	---	1	1	2	1	2	2	6	2	2	30/27	90.0%
	---	50%	---	---	---	100%	100%	100%	---	100%	---	0%	100%	100%	100%	50%	100%	100%	100%	100%		
P. palliata	---	---	---	---	---	---	---	1	1	---	---	---	1	1	4	---	---	---	---	---	8/8	100%
	---	---	---	---	---	---	---	100%	100%	---	---	---	100%	100%	100%	---	---	---	---	---		
P. tarsius	---	---	---	---	1	1	---	---	---	---	---	---	---	1	7	1	1	---	---	---	12/12	100%
	---	---	---	---	100%	100%	---	---	---	---	---	---	---	100%	100%	100%	100%	---	---	---		
P. tomopterna	---	---	---	---	---	---	---	---	---	---	---	---	---	---	3	---	---	---	---	---	3/3	100%
	---	---	---	---	---	---	---	---	---	---	---	---	---	---	100%	---	---	---	---	---		
P. vaillanti	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	2	---	---	2/1	50.0%
	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	50%	---	---		
S. carneus	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1	---	---	---	---	---	1/1	100%
	---	---	---	---	---	---	---	---	---	---	---	---	---	---	100%	---	---	---	---	---		
C. midas	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1/1	100%
	100%	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
C. bassleri	---	---	---	---	---	---	---	---	---	---	1	---	---	---	---	---	1	---	---	---	2/1	50.0%
	---	---	---	---	---	---	---	---	---	---	100%	---	---	---	---	---	0%	---	---	---		
H. boliviana	---	---	---	---	---	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	1/1	100%
	---	---	---	---	---	---	100%	---	---	---	---	---	---	---	---	---	---	---	---	---		
R. palmipes	1	1	5	---	2	5	---	2	1	---	---	4	3	---	1	3	---	2	---	---	30/25	83.3%
	100%	100%	100%	---	100%	100%	---	100%	100%	---	---	25%	100%	---	0%	100%	---	50%	---	---		

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